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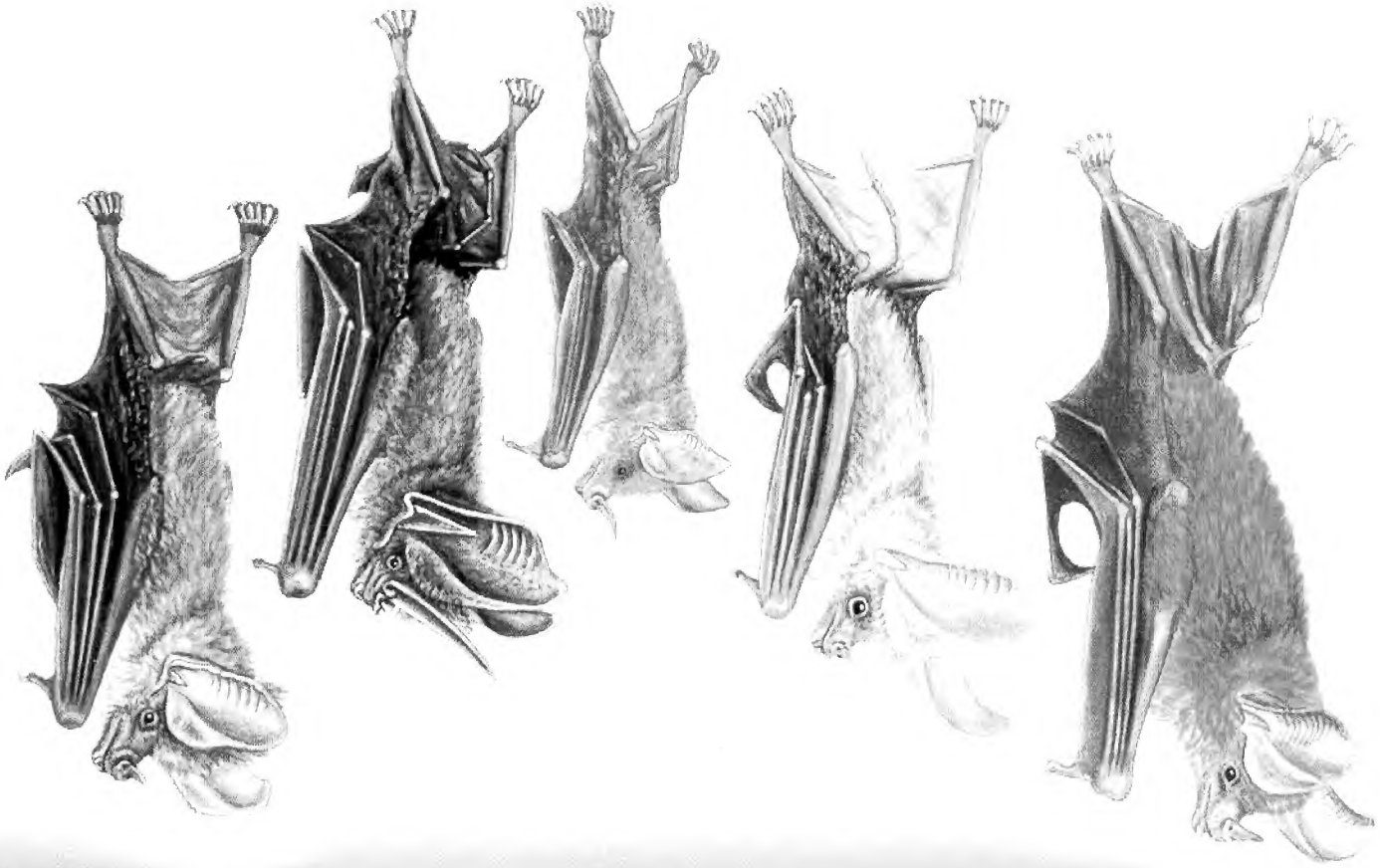

Diversification among New World Leaf-Nosed Bats: An Evolutionary Hypothesis and Classification Inferred from Digenomic Congruence of DNA Sequence

ABSTRACT

We assessed phylogenetic relationships among 48 of 53 genera of phyllostomid bats based on mitochondrial DNA (mtDNA) sequence data encompassing three adjacent genes (12S rRNA, $tRNA^{Val}$, 16S rRNA). We employed Bayesian methods to produce an mtDNA tree, to reanalyze the nuclear Recombination-Activating Gene-2 (*RAG2*) sequence data, and to produce a tree of concatenated mtDNA and *RAG2* data. We compared these gene trees with a recent total-evidence phylogeny based primarily on morphology. The congruence across all three trees (mtDNA, *RAG2*, total-evidence), was 16 of 55 nodes with identical content. The majority of incongruencies involved nodes that were weakly supported in the total-evidence tree. There was greater congruence between data sets from the mitochondrial and nuclear genomes, with 37 of 55 nodes identical in content. Analysis of the concatenated molecular data (about 4.0 kilobases) produced nearly identical branching patterns but with higher statistical support. Forty-eight of 55 generated clades received Bayesian posterior probabilities ≥ 0.95 and 42 had a probability of 1.00. The seven weakly-supported clades occurred in the middle or terminal part of the tree. We interpret the Bayesian posterior probability values as well as the observation that the total number of shared nodes (37 of 55) between the gene trees (support from two independent genomes) as strong evidence that these nodes, as identified, have a high probability of reflecting evolutionary relationships. We contend that digenomic congruence with concomitant statistical support is a robust statement in phylogeny reconstruction. Using the molecular and total-evidence trees and other information (e.g., karyotypes), we developed a higher-level classification for the family Phyllostomidae that includes 56 genera in 11 subfamilies: Macrotinae, Micronycterinae, Desmodontinae, Lonchorhininae, Phyllostominae, Glossophaginae, Lonchophyllinae, Carolliinae, Glyphonycterinae, Rhinophyllinae, and Stenodermatinae. Our arrangement differs substantially from previous classifications. For example, members of the traditional subfamily Phyllostominae are divided into five subfamilies.

Front cover: Artwork by Fiona Reid depicting the five lineages of the former Phyllostominae that are representative of subfamilies in the classification proposed herein. Taxa (from left to right) are: *Micronycteris hirsuta*, *Lonchorhina aurita*, *Trinycteris nicefori*, *Macrotus californicus*, and *Tonatia saurophila*.

Diversification among New World Leaf-Nosed Bats: An Evolutionary Hypothesis and Classification Inferred from Digenomic Congruence of DNA Sequence

Robert J. Baker, Steven R. Hoofer, Calvin A. Porter, and Ronald A. Van Den Bussche

The family Phyllostomidae constitutes a large and diverse complex of bats (53 genera and about 141 species; Wetterer et al. 2000; their Table 7, Pp. 138-139) that exhibits more variation in morphological features than any other family-level group of mammals. Members of this family have modifications for insectivory, frugivory, nectivory, sanguivory, as well as other modifications generally associated with omnivory. This diversity has been problematic for systematists, hindering efforts to reconstruct the phylogenetic history of the group. As a consequence, the systematics of Phyllostomidae has been studied for more than a century without consensus (Wetterer et al. 2000). Studies of phyllostomid relationships make up more than one-third of all studies of bat systematics (Jones et al. 2002).

Wetterer et al. (2000) recently examined morphology and much of the data available in the literature to produce a total-evidence tree (Fig. 1; hereafter referred to as the "total-evidence" tree) for all phyllostomid genera currently recognized. Their study represents the most comprehensive cladistic treatment of morphological data for a mammalian family. Jones et al. (2002) employed the Matrix Representation using Parsimony (MRP) method for phylogeny reconstruction of Phyllostomidae, a method that loosely corresponds to a majority-rule consensus among published cladograms (and sometimes dubbed "super"-tree analysis). Their tree (Fig. 2; hereafter referred to as the "MRP" tree) most closely matches the total-evidence tree, probably because it was largely based on the data and studies reviewed by Wetterer et al. (2000); however, some differences in topology are evident (compare Figs. 1 and 2). Baker et al. (2000) performed a cladistic analysis on DNA sequence data from the nuclear Recombination Activating Gene-2 (*RAG2*) for 66 taxa representing all but five genera (Fig. 3; hereafter referred to as the "*RAG2*" tree). Deep branching patterns in the *RAG2* tree differed markedly from those in the total-evidence tree and from most previous systematic hypotheses.

Our goals were to discriminate between alternative phylogenetic hypotheses for phyllostomid bats (e.g., Baker et al. 1989, 2000; Wetterer et al. 2000; Jones et al. 2002) by examining mitochondrial DNA (mtDNA) sequences (about 2.6 kilobases) encompassing three genes (12S rRNA, $tRNA^{Val}$, 16S rRNA) and, if appropriate, to examine relationships based on concatenation of the mtDNA and *RAG2* sequences (about 4.0 kilobases). We chose the mitochondrial ribosomal genes for several reasons: 1) they should not be linked to the nuclear genome, providing data independent of *RAG2* sequences, 2) they represent the phylogenetic signal present within the mitochondrial genome (Cummings et al. 1995), 3) they should provide a genealogic estimate largely uncorrelated with morphological adaptations of phyllostomids, and 4) they have been used successfully to infer relationships among other bat taxa with similar levels of divergence as well as in other mammals (e.g., Hixon and Brown 1986; Allard and Honeycutt 1992; Frye and Hedges 1995; Van Den Bussche and Hoofer 2000, 2001; Hoofer and Van Den Bussche 2001, 2003).

Production of our mtDNA tree creates a new and welcomed situation for phyllostomid systematics. Three different hypotheses (=trees) now exist for nearly all putative genera, each derived by explicit phylogenetic analysis of independent and primary data sources: 1) primarily skeletal and soft anatomy but in reality a complex collection of data sources (Wetterer et al. 2000); 2) a nuclear gene (Baker et al. 2000); and 3) mitochondrial ribosomal genes (this paper). The ultimate goal of this study was to develop a Linnaean classification for higher-level taxa within the Phyllostomidae that incorporates information from all three data sources. We contend that relationships supported by all three data sources have a high probability of representing monophyletic lineages and should be recognized in any classification proposed for the family. Similarly, relationships supported in two of the three trees also should be recognized as monophyletic assemblages until additional, independent data are provided with support to the contrary.

Baker et al., 2003. Evolutionary Relationships and Classification of New World Leaf-Nosed Bats Inferred from DNA Sequence
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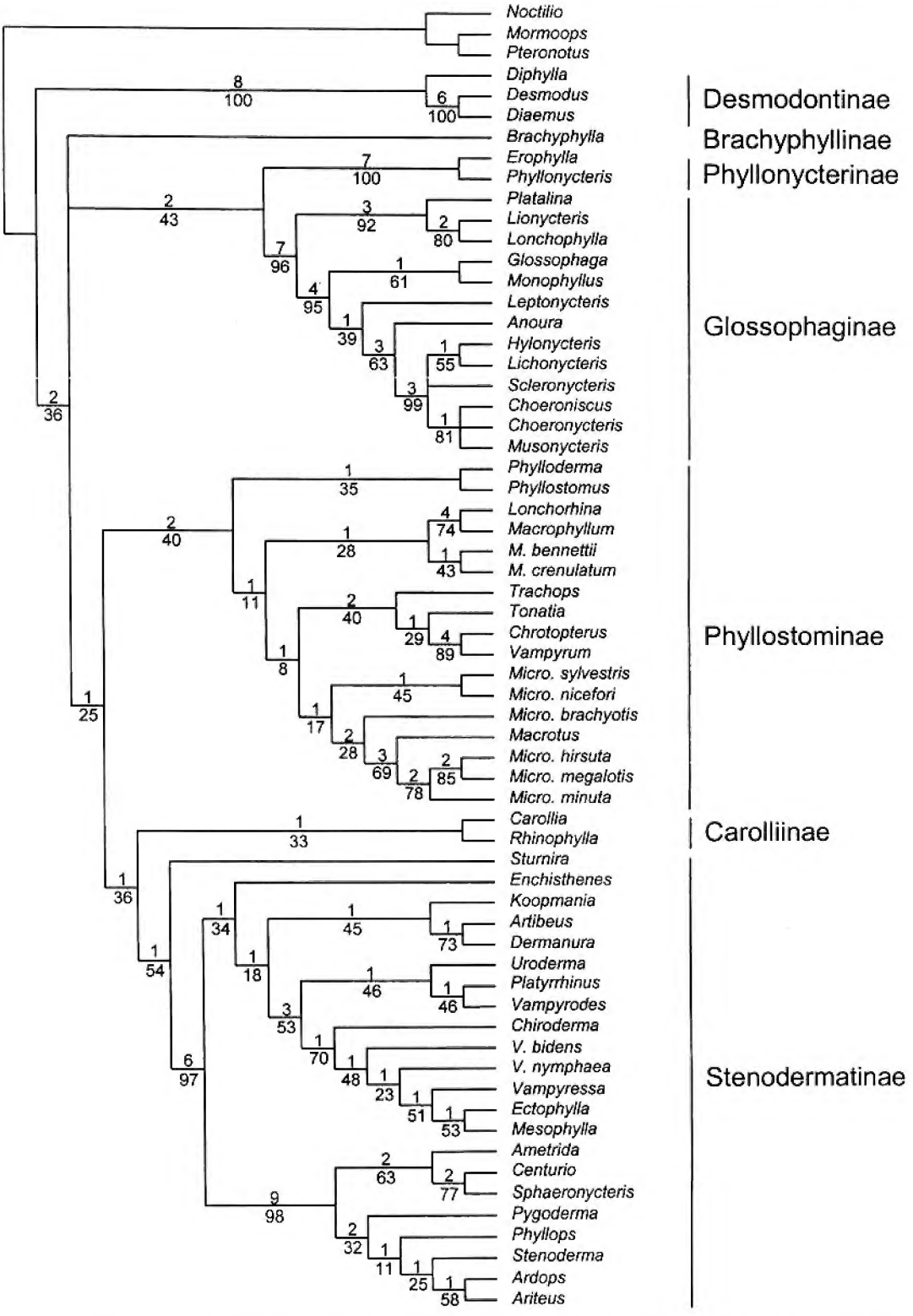


Figure 1. Total-evidence tree of Wetterer et al. (2000) from parsimony analysis of 150, primarily morphologic, characters for 63 taxa (redrawn from their Fig. 49). Numbers above branches are decay values; those below are percent bootstrap values. We added their subfamily classification to the right. *M.* = *Mimon*, *Micro.* = *Micronycteris*, *V.* = *Vampyressa*.

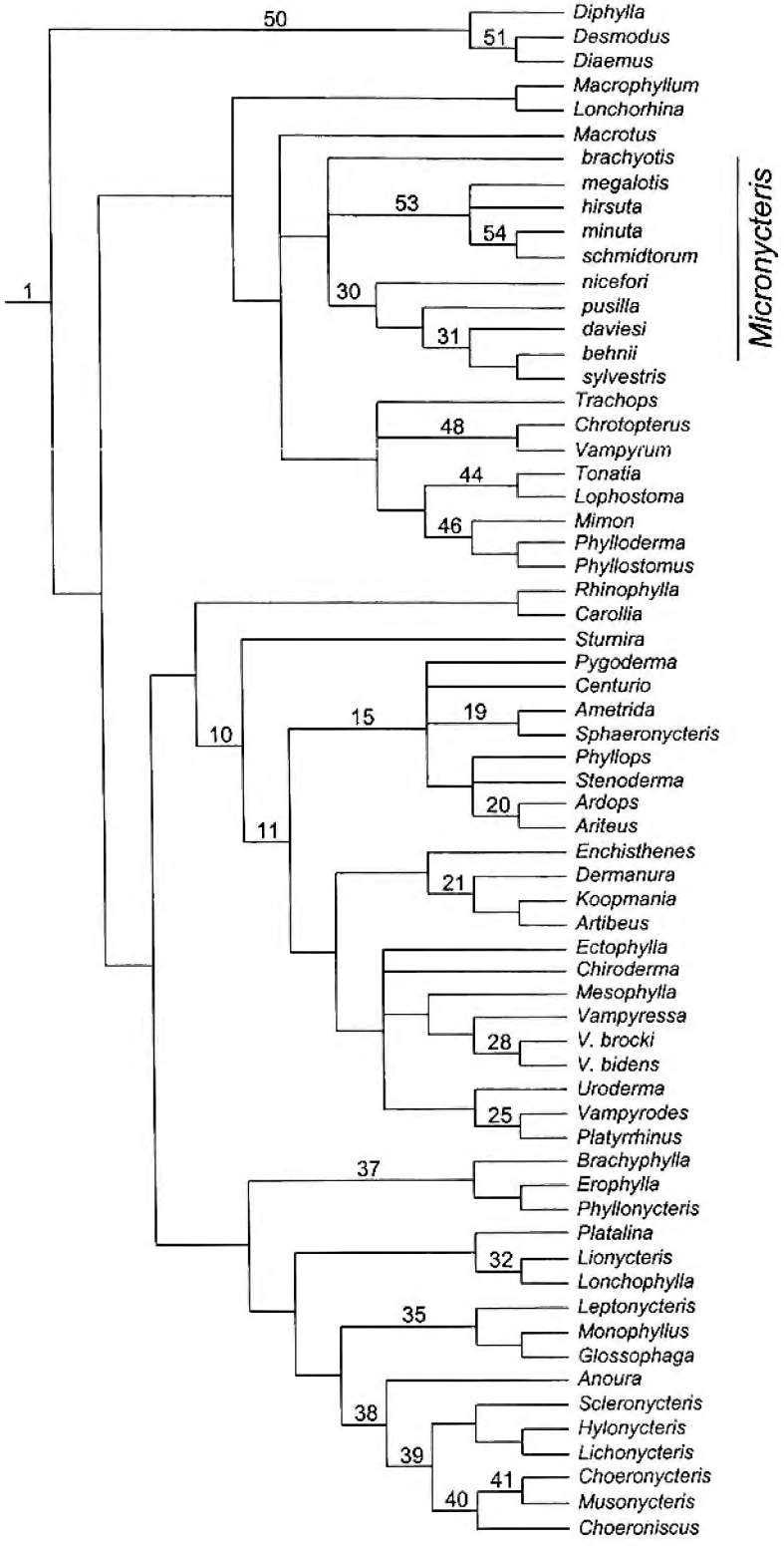


Figure 2. Matrix Representation using Parsimony (MRP) tree of Jones et al. (2002) redrawn from their figure 3 (a-c), showing the relationships of genera that are recognized or discussed in our text. Numbers identify the presence of that clade in Table 1. *V.* = *Vampyressa*.

MATERIALS AND METHODS

mtDNA data collection and analysis. —We obtained tissue samples from wild-caught individuals representing all genera recognized by Koopman (1993, 1994) (see specimens examined and Wetterer et al. 2000) except for *Lichonycteris*, *Phyllonycteris*, *Phyllops*, *Platalina*, and *Scleronycteris*. We obtained 23 mtDNA sequences from GenBank, which we (SRH, RAVDB) had generated in previous studies. We examined multiple species of *Micronycteris, Tonatia,* and *Vampyressa* because their monophyly has been questioned (e.g., Wetterer et al. 2000; Lee et. al. 2002). We followed standard methods to extract genomic DNA from skeletal muscle or organ tissue samples (Longmire et al. 1997) and to PCR amplify and sequence the 12S rRNA, $tRNA^{Val}$, 16S rRNA genes entirely in both directions with an assortment of external and internal primers (Van Den Bussche and Hoofer 2000).

Several parameters can affect alignment of multiple ribosomal DNA sequences and , therefore, phylogeny reconstruction (e.g., see Lutzoni et al. 2000). In this study, we followed the methods of Hoofer et al. (2003), who performed two multiple sequence alignments in CLUSTAL X software (Thompson et al. 1997), one with the default gap-cost ratio (15.00:6.66), the other with a smaller ratio (5:4). Both were refined by eye according to secondary structural models (Anderson et al. 1982; De Rijk et al. 1994; Springer and Douzery 1996).

We coded nucleotides as unordered, discrete characters (G, A, T, C), multiple states as polymorphisms, and gaps as missing, and inferred phylogenetic relationships by Bayesian analysis (Li 1996; Mau 1996; Rannala and Yang 1996) implemented in MrBayes 2.01 (Huelsenbeck and Ronquist 2001). We chose Bayesian analysis over other optimality criteria (i.e., maximum likelihood, maximum parsimony) because it is quick and efficient for large data sets, provides reliability estimates (i.e., branch support) by straightforward posterior probabilities, and utilizes a statistically robust procedure to extract the maximum amount of information from the sequence data (Whelan et al. 2001). We analyzed the 2.6-kilobase fragment of mtDNA as a single unit, rather than by each gene separately, because several studies have demonstrated homogeneity among the three genes (Van Den Bussche and Hoofer 2000, 2001; Hoofer and Van Den Bussche 2001; Van Den Bussche et al. 2002; Hoofer et al. 2003), and all mitochondrial genes are linked and should have identical phylogenetic histories (Brown 1985; Wiens 1998).

We ran all Bayesian analyses at least 1×10^6 generations with one cold and three incrementally heated Markov chains, with starting trees for each chain being random in origin, and trees saved every 10 generations. We ran three independent analyses designating *Saccopteryx* (Emballonuridae) as the outgroup to assess whether chains converged on the same posterior probability distribution and whether likelihoods reached stable values (Huelsenbeck et al. 2002). We estimated burn-in values (initial set of unstable generations to be ignored) by empirical evaluation of likelihoods. The general time reversible model of sequence evolution (GTR) with allowances for a gamma distribution of rate variation (Γ) and for proportion of invariant sites (I) best fit the mtDNA data (Modeltest; Posada and Crandall 1998). We did not define model parameters *a priori*, but treated them as unknowns (with uniform priors) to be estimated in each Bayesian analysis (Leaché and Reeder 2002).

Conditional combination of mtDNA and RAG2 data.—We assessed combinability of mtDNA and *RAG2* data sets following Wiens (1998; see also Leaché and Reeder 2002). To do this, we re-analyzed the *RAG2* data with Bayesian methods (as described above) and the GTR + Γ + I model (Modeltest; Posada and Crandall 1998), and relied on parametric posterior probabilities from Bayesian analysis ($P \geq 0.95$) to indicate statistically supported relationships (Wiens 1998). However, because we were able to generate (or obtain from GenBank) mtDNA sequences for most, but not all, taxa examined by Baker et al. (2000), we truncated the *RAG2* data set to include only those taxa shared between studies, reducing our operational taxonomic units to 62 (56 phyllostomids and six outgroups). Nonetheless, all subfamilies and tribes as well as unranked taxa of Baker et al. (1989, 2000) and Wetterer et al. (2000) were represented.

Classification.—We develop a classification for Phyllostomidae through taxonomic congruence between three independent phylogenies (mtDNA, *RAG2*, and total-evidence) or between any two of the three. That is, we recognized a taxon for each clade shared between all three phylogenetic trees, for most clades supported in two of the three trees and for most clades supported in the concatenated gene tree and one of the two gene trees. In the latter situations, we recognized taxa with statistically supported relationships (i.e., posterior probabilities ≥ 0.95) and information from other data sources (e.g., karyotypes).

RESULTS

Re-analysis of RAG2 data.—All sequences generated in this study are deposited in GenBank (see Appendix 1, Specimens Examined). Bayesian likelihoods for the *RAG2* data of Baker et al. (2000) reached stationarity at 50,000 generations (burn-in = 5,000) reducing the number of sampled trees to 95,000. Topologies and posterior probabilities for nodes and model parameters for all three runs were in excellent agreement. There was close agreement between the Bayesian tree (Fig. 3) and the Maximum Parsimony tree of Baker et al. (2000, their Fig. 2).

mtDNA data.— Alignment (default settings) of the 59 mtDNA sequences that we generated plus the 23 obtained from GenBank resulted in 2,804 aligned sites. We excluded 544 characters from all analyses because positional homology was ambiguous (Hoofer and Van Den Bussche 2003), resulting in 2,260 sites for phylogenetic analysis. Most ambiguous sites were within loop regions of the ribosomal genes, but some were in stem regions and within the tRNA gene. Alignment using the smaller gap-cost ratio (5:4) was slightly longer than the default alignment, with more gaps inserted primarily in large loop regions of the ribosomal genes. There were slightly more ambiguous characters in the 5:4 alignment corresponding to the increased number of inserted gaps in variable loop regions.

Bayesian likelihoods reached stationarity at 50,000 generations (burn-in = 5,000) reducing the sampled trees to 95,000. Topologies (Fig. 4) and posterior probabilities for nodes and model parameters for all three runs were in excellent agreement. Analyses with both alignments also produced identical topologies and nearly identical posterior probabilities. There were no supported conflicts ($P \geq 0.95$) between results from Bayesian analyses of mtDNA and *RAG2* data; therefore, we combined the data sets.

Combined data.—The combined alignment of mtDNA and *RAG2* data resulted in 4,164 characters, of which 3,620 were utilized in the phylogenetic analysis. Bayesian likelihoods reached stationarity at 20,000 generations (burn-in = 2,000) reducing the number of sampled trees to 98,000. Topologies and posterior probabilities for nodes and model parameters for all three runs again were in excellent agreement.

There was statistical support for the majority of clades in the combined gene tree (Fig. 5*a*; hereafter referred to as the "combined gene tree"). Forty eight of 55 generated clades received posterior probabilities ≥0.95 and 42 had a probability of 1.00. The seven weakly-supported clades occurred in the middle or terminal part of the tree (Table 1; Fig. 5*a*). All 55 nodes (Fig. 5*a*) are numbered for identification in text with Bayesian probabilities given in Table 1. The majority of the 55 nodes in the combined gene tree also was supported by independent analyses of the mtDNA and *RAG2* data (Table 1); 39 of 55 for mtDNA (Fig. 4) and 30 of 55 for *RAG2* received posterior probabilities ≥0.95 (Fig. 3). Nodes that are present in the total-evidence tree (Fig. 1), *RAG2* tree (Fig. 3), and mtDNA tree (Fig. 4) are mapped onto our combined gene tree, indicated by the letters M, R, and T, respectively (Fig. 5*a*).

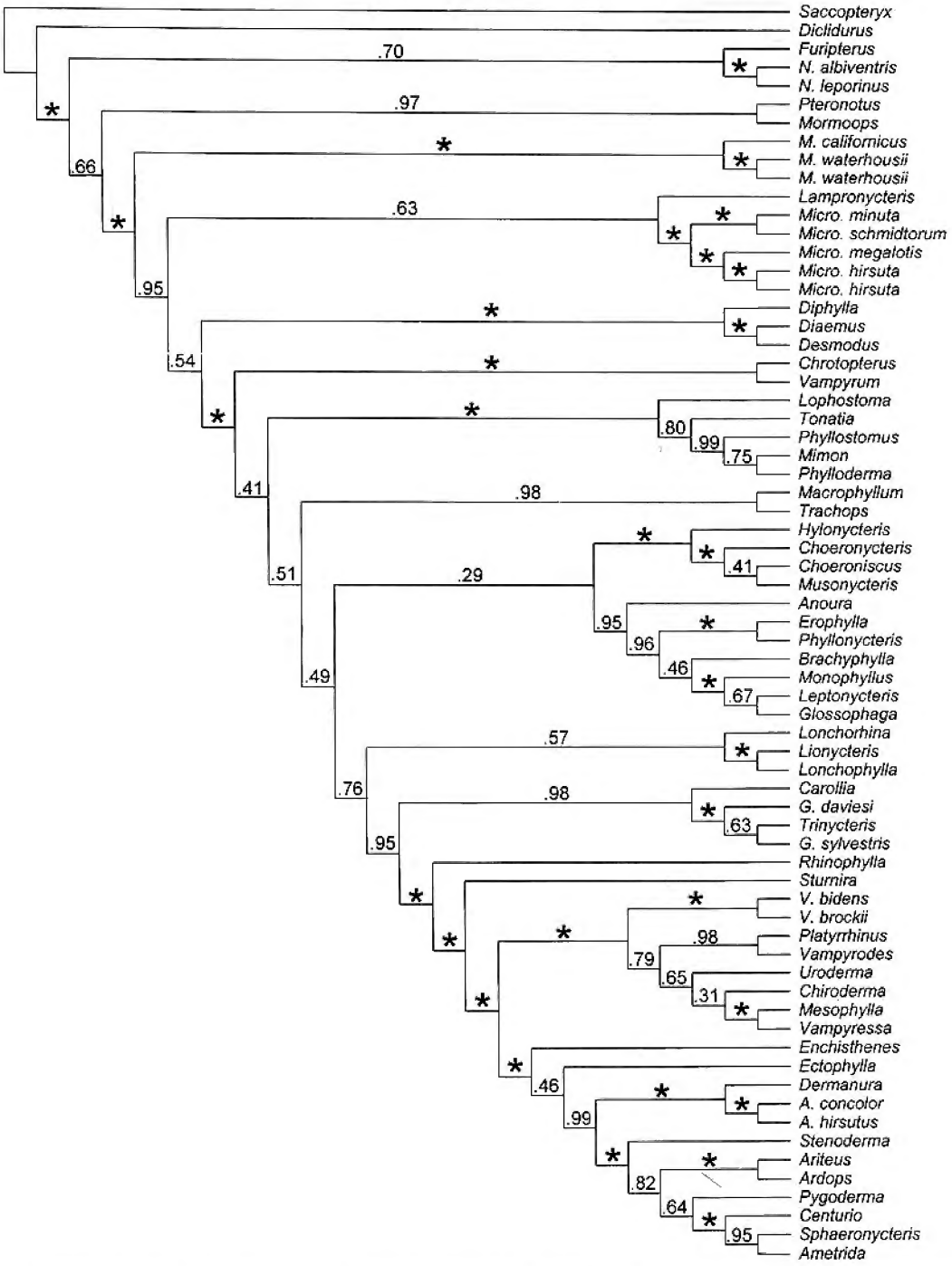


Figure 3. Cladogram for Phyllostomidae from Bayesian analysis (GTR + Γ + I) of *RAG2* data. Numbers are posterior probabilities; * signifies a probability of 1.00. Mean model parameters were: Lnl, -9699.677; R_{CT}, 10.085; R_{CG}, 1.302; R_{AT}, 0.649; R_{AG}, 8.138; R_{AC}, 1.813; π_A, 0.288; π_C, 0.227; π_G, 0.232; π_T, 0.253; α, 0.765; P_{inv}, 0.360. Our results are essentially identical to those from the original parsimony analysis by Baker et al. (2000; their Fig. 2), although we included one additional phyllostomid, *Vampyriscus brocki*. We re-analyzed the *RAG2* data with Bayesian methods to assess conditional combination of the *RAG2* and mtDNA data sets. *A.* = *Artibeus*, *G.* = *Glyphonycteris*, *M.* = *Macrotus*, *Micro.* = *Micronycteris*, *N.* = *Noctilio*, *V.* = *Vampyriscus*. Generic designations follow the classification proposed in this paper.

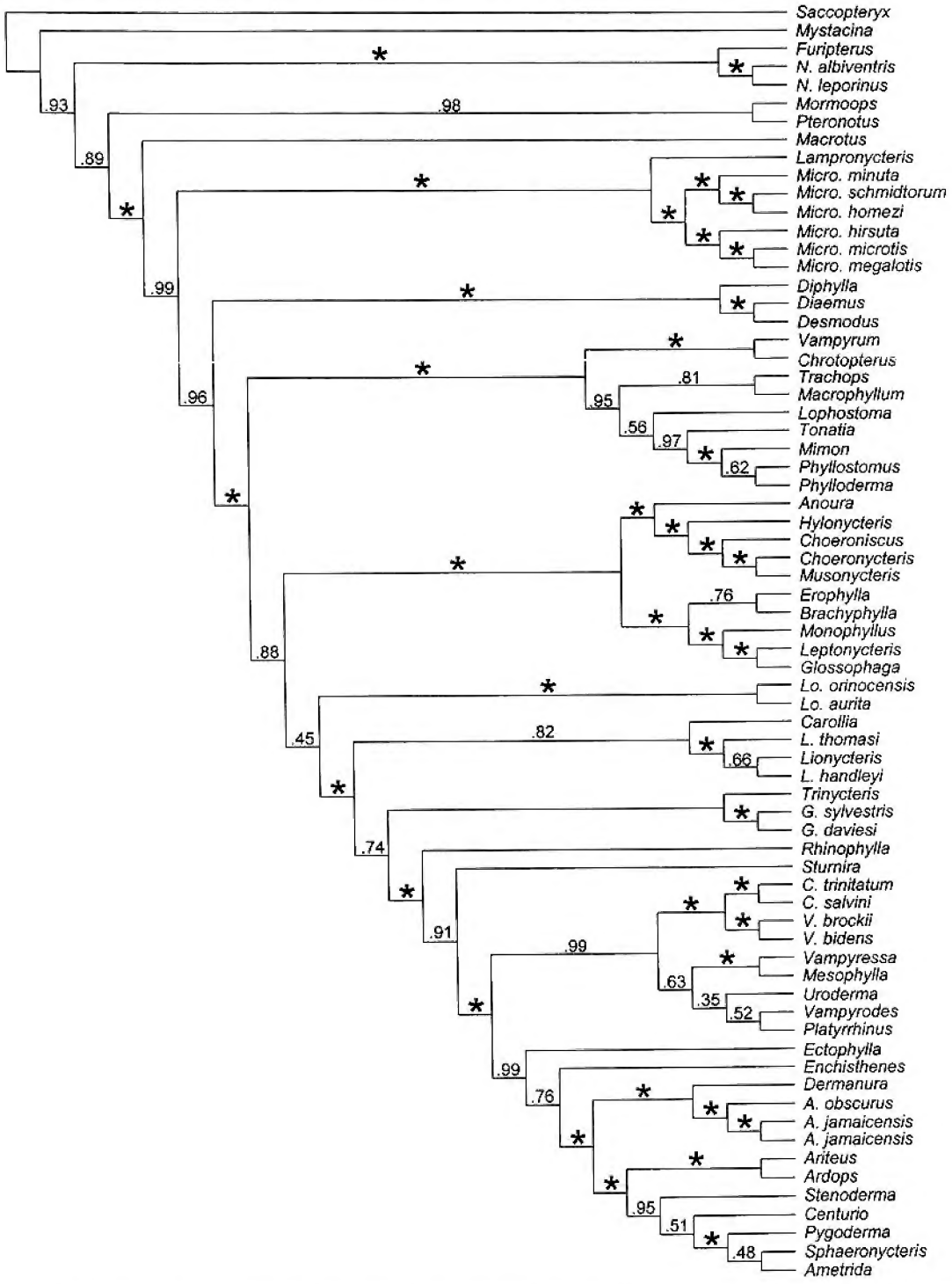


Figure 4. Cladogram for Phyllostomidae from Bayesian analysis (GTR + Γ + I) of the mitochondrial 12S rRNA, $tRNA^{Val}$, and 16S rRNA genes. Numbers are posterior probabilities; * signifies a probability of 1.00. Mean model parameters were: Lnl, -27467.426; R_{CT}, 53.717; R_{CG}, 0.657; R_{AT}, 3.465; R_{AG}, 16.377; R_{AC}, 4.687; π_A, 0.365; π_C, 0.224; π_G, 0.182; π_T, 0.229; α, 0.616; P_{inv}, 0.439. *A.* = *Artibeus*, *C.* = *Chiroderma*, *G.* = *Glyphonycteris*, *L.* = *Lonchophylla*, *Lo.* = *Lonchorhina*, *Micro.* = *Micronycteris*, *N.* = *Noctilio*, *V.* = *Vampyriscus*. Generic designations follow the classification proposed in this paper.

DISCUSSION

Molecular and morphological congruence.—There are 16 nodes shared in the three independent data sets (Table 1; total-evidence, Fig. 1; *RAG2*, Fig. 3; mtDNA, Fig. 4), which we contend have the highest probability of being monophyletic assemblages. Of these, eight unite sister genera or species within a genus. Thus, congruence among all three data sets provides little resolution to the deep branching patterns or the evolutionary relationships among the diverse, morphological extremes associated with variation in feeding strategies. Comments on each node follow (Table 1, Fig. 3 and Fig. 5*a*).

First, the monophyly of the family Phyllostomidae (node 1) is supported in all three trees. This is critical to the assumption that the tremendous diversity in morphology, feeding strategies, chromosomal evolution, etc. is attributed to evolutionary events occurring since common ancestry and not the result of combining unnatural assemblages. This conclusion also is critical to many studies of character transformation (e.g., McDaniels 1976; Hood and Smith 1982; Bhatnager 1985; Ferrarezzi and Gimenez 1996; Freeman 1998). Second, the monophyly of the vampire bats (node 50) is supported in all three trees. This clade is the most constant feature on which studies of phyllostomid systematics agree, with it appearing in nearly all previous classifications. Also, the basal relationship of *Diphylla* to *Diaemus* + *Desmodus* is present in all three trees (node 51).

The monophyly of the Stenodermatinae (node 10) is indicated in all three data sets. Although *Sturnira* has been placed into its own subfamily (Sturnirinae; Miller 1907), Baker (1967) concluded that *Sturnira* was a member of the Stenodermatinae based on chromosomal data from nondifferentially stained karyotypes. Unpublished G-band data also are explained most parsimoniously by *Sturnira* being an ingroup to the Stenodermatinae after diverging from the remainder of the Phyllostominae. Node 11 is common to all three trees and documents a basal position for *Sturnira* relative to the remainder of the Stenodermatinae.

Within node 10, there are differences in branching patterns among trees but four clades are common to all trees. There has been general agreement that the short-faced, white-shouldered taxa, *Stenoderma*, *Ariteus*, *Ardops*, *Pygoderma*, *Centurio*, *Sphaeronycteris*, and *Ametrida* (also *Phyllops* based on morphology; Wetterer et al. 2000), form a natural assemblage. The presence of node 15 in all three trees supports this conclusion. Within the short-faced bats a clade indicating a sister relationship of *Ariteus* and *Ardops* is indicated in all three trees (node 20). Also within the Stenodermatinae the sister relationship of *Artibeus* and *Dermanura* (node 21) and of *Platyrrhinus* and *Vampyrodes* (node 25) is indicated. Node 25 also is supported in the molecular data (Van Den Bussche et al. 1998) and morphological data presented by Lim (1993).

Within the nectar-feeders, a clade (node 39) common to all three trees contains the genera *Hylonycteris*, *Choeroniscus*, *Choeronycteris*, and *Musonycteris*. Within this clade, node 40 exists in all three trees indicating a basal position for *Hylonycteris* relative to the other three genera.

The genus *Micronycteris* (*sensu stricto*, Wetterer et al. 2000) is indicated by node 53, which is represented by various subsets of species in each of the three trees. Because the number of sampled species of *Micronycteris* varies among trees, interpretation of sister relationships within node 53 is limited. However, the monophyly of the group as recognized by Wetterer et al.(2000) receives support. Node 55 is present in all three trees and indicates a sister level relationship for the species *M. hirsuta* and *M. megalotis*. Other sister relationships for pairs of genera indicated in the three trees include *Glyphonycteris* and *Trinycteris* (node 30), *Lionycteris* and *Lonchophylla* (node 32), and *Vampyrum* and *Chrotopterus* (node 48).

Digenomic congruence.—No additional nodes are shared between the *RAG2* and the total-evidence trees, and only a single additional node was shared between the mtDNA and total-evidence trees. This node (38), which places *Anoura* at the base of the taxa in node 39 noted above (Fig. 5*a*), received statistical support in the mtDNA and combined gene trees but not in the *RAG2* Bayesian tree (Table 1). Node 38 also was present in the *RAG2* parsimony tree (Baker et al. 2000).

In contrast, there are 21 additional nodes shared between the two gene trees (Figs. 3 and 4) that are not

*Table 1.—Taxonomic congruence and statistical support among selected studies of phyllostomids: mtDNA + RAG2, this study; mtDNA, this study; Bayesian analyzed RAG2 data of Baker et al. (2000); total-evidence (primarily morphologic data), Wetterer et al. (2000); and Matrix Representation using Parsimony (MRP) analysis of published trees, Jones et al. (2002). Nodes 1—55 correspond to the combined gene tree (mtDNA + RAG2 data; Fig. 5). Levels of statistical support from the combined data analysis and from analyses of independent data sets are given for each node (if present); support values from molecular analyses are Bayesian posterior probabilities, whereas values from the total-evidence study are bootstrap proportions. – indicates that the node was not present. Nodes in the MRP tree and nodes shared among all trees are indicated by an X. Node 1 in the total evidence tree was present, but no bootstrap values were reported. Taxa identified for each node (where applicable) are those in the classification proposed in this paper. * denotes unranked names.*

Node	Taxon	mtDNA + *RAG2*	mtDNA	*RAG2*	Total-evidence	MRP	Shared in all trees
1	Phyllostomidae	1.00	1.00	1.00	X	X	X
2	Karyovarians*	0.97	0.96	0.95	-	-	-
3	Victivarians*	0.97	1.00	0.54	-	-	-
4	Phyllovarians*	1.00	0.96	1.00	-	-	-
5	Unnamed*	0.96	-	-	-	-	-
6	Hirsutaglossa*	1.00	-	-	-	-	-
7	Dulcivarians*	0.99	1.00	-	-	-	-
8	Nullicauda*	1.00	-	0.95	-	-	-
9	Carpovarians*	1.00	1.00	1.00	-	-	-
10	Stenodermatinae	1.00	0.91	1.00	54	X	X
11	Stenodermatini	1.00	1.00	1.00	97	X	X
12	Mesosternodermatini*	1.00	0.99	-	-	-	-
13		0.52	-	0.46	-	-	-
14	Unnamed*	1.00	1.00	-	-	-	-
15	Sternodermatina	1.00	1.00	1.00	98	X	X
16		0.93	0.95	-	-	-	-
17		1.00	0.51	0.64	-	-	-
18		1.00	1.00	-	-	-	-
19		0.87	0.48	0.95	-	X	-
20		1.00	1.00	1.00	58	X	X
21	Artibeina	1.00	1.00	1.00	73	X	X
22	Vampyressina	1.00	0.99	1.00	-	-	-
23		0.53	0.63	-	-	-	-
24		0.72	-	-	-	-	-
25		1.00	0.52	0.98	46	X	X
26		1.00	1.00	1.00	-	-	-
27		1.00	1.00	-	-	-	-
28		1.00	1.00	1.00	-	X	-
29	Unnamed	0.99	-	0.98	-	-	-
30	Glyphonycterinae	1.00	1.00	1.00	45	X	X
31		1.00	1.00	-	-	-	-
32	Lonchophyllinae	1.00	1.00	1.00	80	X	X
33	Glossophaginae	1.00	1.00	0.29	-	-	-
34		1.00	1.00	0.96	-	-	-
35	Glossphagini	1.00	1.00	1.00	-	X	-
36		1.00	1.00	0.67	-	-	-
37		0.97	0.76	-	-	X	-
38	Choeronycterini	1.00	1.00	-	66	X	-
39	Choeronycterina	1.00	1.00	1.00	93	X	X
40		1.00	1.00	1.00	81	X	X
41		1.00	1.00	0.41	-	-	-
42	Phyllostominae	1.00	1.00	-	-	-	-
43		0.54	-	-	-	-	-
44	Phyllostomini	1.00	0.56	1.00	-	X	-
45		1.00	0.97	0.80	-	-	-
46		1.00	1.00	0.99	-	X	-
47		0.48	-	-	-	-	-
48	Vampyrini	1.00	0.81	1.00	89	X	X
49	Macrophyllini	1.00	1.00	0.98	-	-	-
50	Desmodontinae	1.00	1.00	1.00	100	X	X
51	Desmodontini	1.00	1.00	1.00	100	X	X
52	Micronycterinae	1.00	1.00	0.63	-	-	-
53		1.00	1.00	1.00	78	X	X
54		1.00	1.00	1.00	-	-	-
55		1.00	1.00	1.00	85	X	X

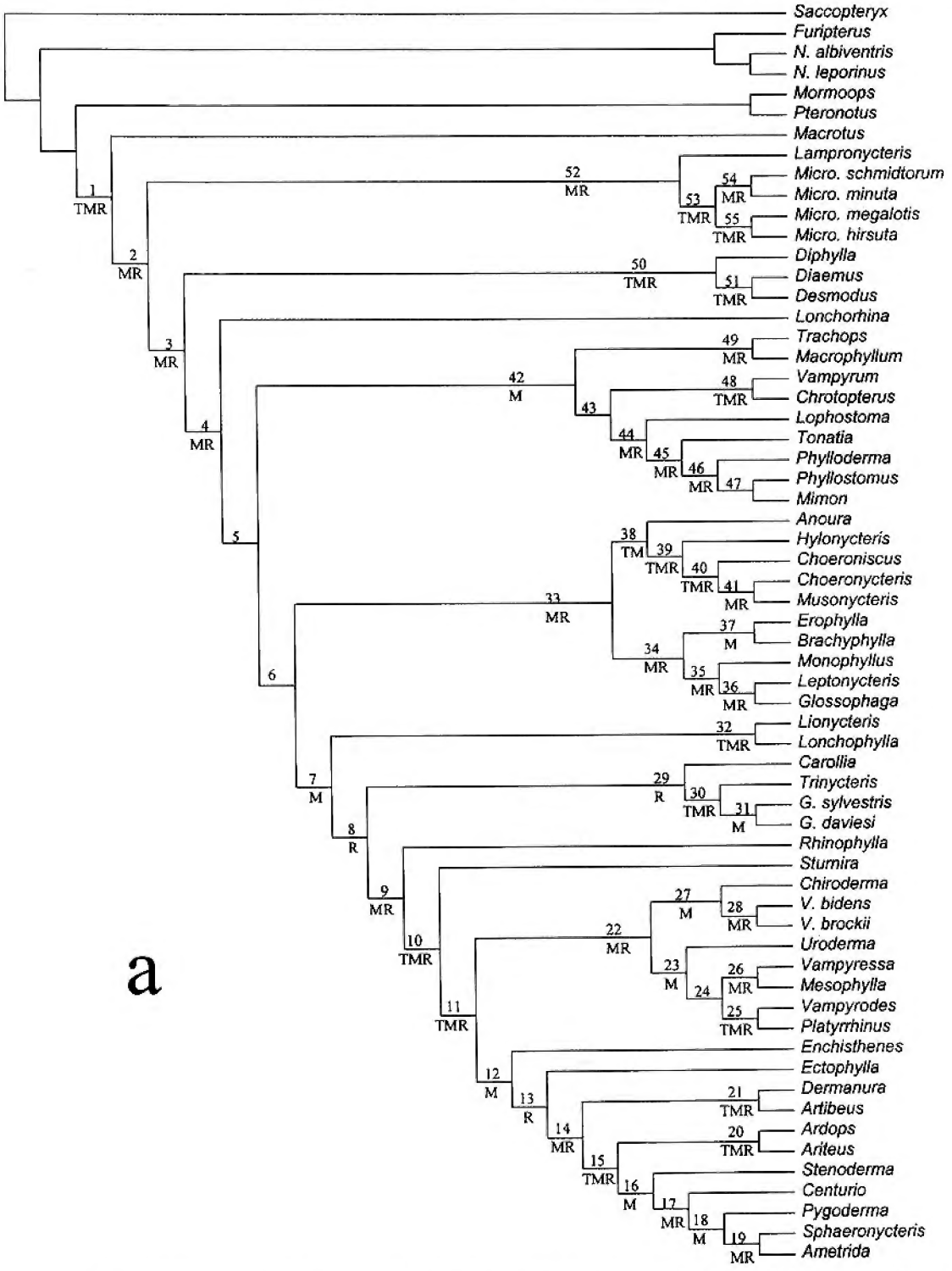
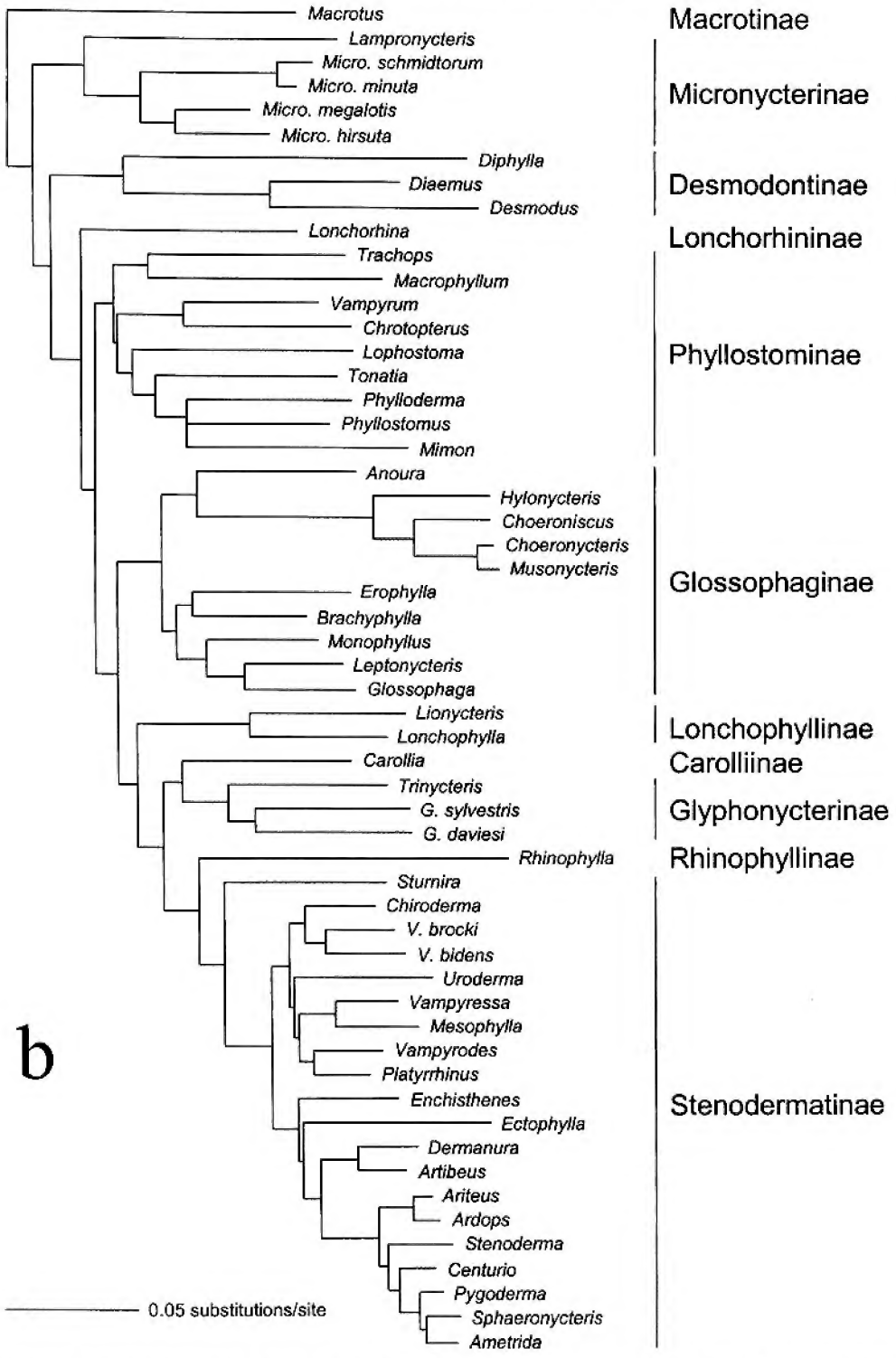


Figure 5. Results from Bayesian analysis (GTR + Γ + I) of concatenated mtDNA and *RAG2* data. Mean model parameters were: Lnl, -40011.880; R_{CT},34.934; R_{CG}, 0.938; R_{AT}, 2.327; R_{AG}, 10.437; R_{AC}, 4.164; π_A, 0.351; π_C, 0.211; π_G, 0.200; π_T, 0.238; α, 0.513; P_{inv}, 0.407. Generic designations follow the classification proposed in this paper. *G.* = *Glyphonycteris*, *Micro.* = *Micronycteris*, *N.* = *Noctilio*, *V.* = *Vampyriscus*. a) Cladogram depicting nodes 1-55. Levels of statistical support for each node from molecular (mtDNA, *RAG2*, and mtDNA + *RAG2*)



and morphological data sets can be found in Table 1. Nodes present in trees produced from independent analysis of mtDNA, *RAG2*, and total-evidence data are denoted by the letters M, R, and T, respectively. b) Phylogram depicting percent sequence divergence among phyllostomid species since their last common ancestor. Our proposed subfamily classification is shown at right. Outgroups were the same but not drawn.

present in the total evidence tree, bringing the total number of shared nodes for the gene trees to 36 of 55. This is a high level of congruence, especially at the base of the tree where resolution has been most difficult to statistically document in previous studies. Of the 36 nodes shared in the two independent gene trees all are present in the combined gene tree (Fig. 5*a*). Of these 36, five also are present in the MRP tree (Table 1).

Possible resolution of the initial branching pattern within phyllostomid bats is present in nodes 2, 3, and 4. This branching sequence indicates that the ancestor of *Macrotus* was the basal divergence for the family (node 2), followed by *Micronycteris* (*sensu* Wetterer et al. 2000; node 3), followed by the ancestor of the vampires (node 4). Most studies have concluded that the vampires were the basal divergence within phyllostomid bats, but within the gene trees there is statistical support for the branching order revealed by nodes 2, 3, and 4. The *Macrotus*, *Micronycteris*, vampire bat order of divergence is a radical departure from the relationships proposed by Wetterer et al. (2000) and Jones et al. (2002). In their trees, the vampires diverged first and *Macrotus* and *Micronycteris* are part of a much larger clade of other morphologically primitive taxa (their Phyllostominae). Within that larger clade in Wetterer et al. (2000), *Macrotus* is central to a group composed of *Micronycteris* (*sensu* Wetterer et al. 2000, p. 141) plus the genera *Trinycteris*, *Glyphonycteris*, and *Lampronycteris* (and possibly *Neonycteris*). Sanborn (1949) and Koopman (1993) recognized the latter four genera as subgenera of *Micronycteris*.

In the gene trees, *Macrotus* is the first clade within the family, *Micronycteris* (*sensu* Wetterer et al. 2000) and *Lampronycteris* compose the second clade within the family, and *Glyphonycteris* and *Trinycteris* diverged distantly within the remainder of the Phyllostomidae (nodes 30, 31; Fig. 5*a*). Thus, our molecular data divide the Micronycterini of Wetterer et al. (2000; *Micronycteris*, *Macrotus*, *Lampronycteris*, *Glyphonycteris*, *Trinycteris*, and *Neonycteris*) into three distantly related clades, for which the common ancestor would have contained all phyllostomid bats.

Using cladistic methods and global parsimony with *Noctilio* and *Mormoops* as outgroups, Patton and Baker (1978) and Baker (1979) proposed that the G-banded karyotype of *Macrotus waterhousii* was identical to that primitive for the family Phyllostomidae. With *Macrotus* central to *Micronycteris*, *Glyphonycteris*, *Lampronycteris*, and *Trinycteris* (all of which have highly rearranged karyotypes), Wetterer et al. (2000) concluded it was improbable that the karyotype of *M. waterhousii* was primitive for the family. Interestingly, the monophyly of the Micronycterini was part of the basis for excluding all chromosomal data from the total-evidence analyses (Fig. 1; Wetterer et al. 2000.) With *Macrotus* being the basal divergence within the family, the molecular data are compatible with the hypothesis that the karyotype of *M. waterhousii* is unchanged from the primitive condition for the family. This conclusion is the foundation for using chromosomal data as synapomorphies to identify clades such as the relationship of *Brachyphylla*, *Erophylla*, *Phyllonycteris*, *Glossophaga*, and *Leptonycteris* (Baker and Bass 1979).

Node 9 unites *Rhinophylla* with the Stenodermatinae. The phylogenetic affinities of *Rhinophylla* have been a source of debate (Wright et al. 1999), but most recent classifications have included *Rhinophylla* and *Carollia* as the only genera in the Carolliinae (Koopman 1993, 1994). There is statistical support in the mtDNA, *RAG2*, and combined gene trees for *Rhinophylla* sharing a common ancestry with the Stenodermatinae after diverging from *Carollia*.

Six additional nodes within the Stenodermatinae are shared by the three gene trees (14, 17, 19, 22, 26, and 28). Node 14 indicates statistical support for *Artibeus* and *Dermanura* sharing a common ancestry with the short-faced bats (node 15) after diverging from the remainder of the Stenodermatinae. Node 17 unites *Centurio*, *Pygoderma*, *Sphaeronycteris*, and *Ametrida*. Node 19 indicates a sister relationship for *Sphaeronycteris* and *Ametrida*. Nodes 17 and 19 received a posterior probability of 0.95 in only one tree. Node 22 unites *Chiroderma*, *Vampyressa*, *Uroderma*, *Mesophylla*, *Vampyrodes*, and *Platyrrhinus*. Genera that, for the most part, are characterized by pelage with a white line down the center of the back. Within this clade, two nodes receive statistical support: node 26, which unites *Vampyressa thyone* and *Mesophylla*; and node 28, which unites *Vampyressa bidens* and *V. brocki*. These two nodes indicate systematic change is needed in content and context of *Vampyressa*. Wetterer et al. (2000) indicated that *Ectophylla* and

Mesophylla are sister taxa and were classified as congeneric. Lim et al. (2003) also indicated that *Ectophylla* and *Mesophylla* are sister taxa but sufficiently divergent morphologically, chromosomally, and genetically to merit generic status. The data in the three gene trees along with chromosomal data (Baker et al. 1973, Greenbaum et al. 1975) indicate that *Mesophylla* and *Vampyressa thyone* are more closely related to each other than to most of the other species in the genus *Vampyressa* as recognized by Koopman (1993). Jones et al. (2002) indicated a sister relationship for *Mesophylla* to the genus *Vampyressa* and Jones et al. (2002) and Lim et al. (2003) concluded that the five species of *Vampyressa* were monophyletic. The monophyly of the genus *Vampyressa* as currently constructed, is questioned in all three gene trees by the placement of *Vampyressa bidens* and *V. brocki* in a clade separate from *Mesophylla* and *V. thyone*.

Relationships within a subset of the nectar-feeders are indicated in node 33, for which molecular data (mtDNA and *RAG2*) are available for 10 genera. In the classification of Wetterer et al. (2000), eight of these genera were part of the Glossophaginae (*Anoura, Hylonycteris, Choeroniscus, Choeronycteris, Musonycteris, Monophyllus, Leptonycteris,* and *Glossophaga*). The other members of node 33 are from another traditional subfamily, Phyllonycterinae, and from the genus *Brachyphylla* (placed as *incertae sedis* by Wetterer et al. 2000). Additionally, Wetterer et al. (2000) included *Lionycteris* and *Lonchophylla* in their Glossophaginae. Here, these two genera are excluded from node 33. Node 34 includes three of the eight genera noted above as part of the Glossophaginae of Wetterer et al (2000), plus a representative of the Phyllonycterinae and *Brachyphylla*. Node 35 separates the three traditional glossophagine genera *Monophyllus*, *Leptonycteris*, and *Glossophaga* from *Brachyphylla* and *Erophylla*. Node 36 indicates a sister relationship for *Leptonycteris* and *Glossophaga*. All three of these nodes, 34, 35, and 36, have statistical support (Table 1). Node 41 indicates a sister relationship between *Choeroniscus* and *Choeronycteris* and is statistically supported in the mtDNA and the combined gene trees (Table 1).

Within part of the Phyllostominae (*sensu* Wetterer et al. 2000) nodes 44, 45, 46, and 49 indicate statistically supported relationships. Node 44 unites *Tonatia*, *Lophostoma*, *Phylloderma*, *Phyllostomus*, and *Mimon*. Node 45 indicates that *Tonatia* (*sensu* Lee et al. 2002) is basal to the other four genera. Node 46 suggests that *Lophostoma* is basal to *Phylloderma*, *Phyllostomus*, and *Mimon*. Node 49 indicates that *Trachops* and *Macrophyllum* are sister, a relationship that has not been proposed. However, *Trachops* and *Macrophyllum* share a feeding strategy of gleaning food from the surface of water, which is unique among phyllostomid bats.

Node 52 unites *Lampronycteris* with *Micronycteris* (*sensu* Wetterer et al. 2000). Node 54 suggests that *Micronycteris schmidtorum* and *M. minuta* are sister taxa; however, several other species of *Micronycteris* have not been analyzed.

Summary and perspective.—The gene trees (Figs. 3 - 5) share more clades with each other than they do with other previously proposed trees and in many ways are incongruent with previous classifications of phyllostomid bats. Perhaps the most striking example involves the subfamily Phyllostominae (*sensu* Koopman 1993, 1994; Wetterer et al. 2000; Jones et al. 2002), a group of bats sharing a suite of morphological character-states that are primitive relative to the remainder of the family. The subfamily Phyllostominae has been troublesome (Smith 1976) and we think has been a "wastebasket taxon" for phyllostomids sharing primitive character states rather than a monophyletic group identified by shared derived character states. Molecular data suggest that this complex of bats is polyphyletic. Members of the Phyllostominae (sensu Koopman 1994, Wetterer et al. 2000, and Jones et al. 2002) are divided by deep branches in the molecular trees, and are part of five independent lineages distributed throughout the family (recognized in our classification as five subfamilies). If the gene trees are accurate, a common ancestor for the traditionally recognized Phyllostominae requires a common ancestor for all phyllostomid bats. Two clades, *Macrotus* (the basal divergence of clade 1) and *Micronycteris*+ *Lampronycteris* (node 52) are basal to the vampires and do not appear to share a common ancestor with each other after diverging from the remainder of the Phyllostomidae. Another portion of the genus *Micronycteris* (*sensu* Jones et al. 2002, node 30) as well as a clade restricted to *Lonchorhina* (the basal branch of node 4) also have statistical support that questions a common ancestry with any other generic level taxon in the Phyllostominae (*sensu* Koopman 1994,

Wetterer et al. 2000 and Jones et al. 2002). There is other evidence of major incompatibilities between the gene trees (Figs. 3-5) on one hand and the two most recent trees generated for the Phyllostomidae on the other (Table 2; Wetterer et al. 2000; Jones et al. 2002). Only two of the seven subfamilies of Wetterer et al. (2000), the Desmodontinae and the Stenodermatinae, and three of eight subfamilies of Jones et al. (2002), the Desmodontinae, Stenodermatinae, and Lonchophyllinae, are monophyletic groups within the gene trees or are not nested within genera proposed for other subfamilies.

Thus, there are several major incongruencies between our gene trees and those based primarily on morphological data. This is especially true if one were to compare our classification with previous classifications (Table 2). However, many of the conflicting relationships are not conflicts when viewed in terms of the level of statistical support for alternatives or, more precisely, for each node upon which the alternative classifications are based (Wiens 1998).

We review the level of support for the gene trees in Table 1. In the combined gene tree, 48 of 55 nodes have a Bayesian posterior probability of ≥0.95, with 42 having a probability of 1.00. We interpret the Bayesian posterior probability values as well as the total number of shared nodes (37 of 55) between the mitochondrial and nuclear gene trees (support from two independent genomes) as strong evidence that these nodes, as identified, have a high probability of reflecting evolutionary relationships. We contend that digenomic congruence with concomitant statistical support is a robust statement in phylogeny reconstruction.

What is the statistical evidence supporting alternative trees in Wetterer et al. (2000) and Jones et al. (2002)? Wetterer et al. (2000) provided bootstrap values, decay values, and their complete data set. In short, we agree with Wetterer et al. (2000; pp. 132-135, 172) that there is weak support for much of the branching order in their tree and (by implication) their classification. Bootstrap values for the 55 nodes in the total-evidence tree are ≥80 in 13 nodes and ≥70 in five others (Fig. 1). Support based on Bremer's (1988) decay method also was limited, with 41 of 55 nodes collapsing in one or two additional steps. The total-evidence offers "weak" support for monophyly of their Phyllostominae (Fig.1; bootstrap value = 40%, decay value = 2), which probably encompasses the majority of differences between our study and theirs. There also is little support in the total-evidence tree for the clade linking their Phyllostominae to the remaining phyllostomids excluding the vampires (bootstrap value = 36, decay value = 2), for the internal node uniting *Macrotus* and *Micronycteris* (*sensu* Wetterer et al. 2000) (bootstrap value = 69, decay value = 3), and for the node separating *Micronycteris sylvestris* and *M. nicefori* from *Macrotus* and the remainder of *Micronycteris* (bootstrap value = 17, decay value = 1).

Even though the study of Wetterer et al. (2000) probably represents the most comprehensive thus far to address the relationships of phyllostomid bats or any mammalian family, there apparently are insufficient morphological synapomorphies within their data set for robust resolution of the deep branching patterns within the Phyllostomidae. This is exemplified by the low level of support for the deep branching patterns in the total-evidence tree (Fig. 1). Perhaps new synapomorphies will be discovered, resulting in more robust support, as the missing data points in the total-evidence matrix are scored and analyzed. This condition is true for chromosomal rearrangements as well (Baker et al. 1989). For example, there are no morphological character-states (including G-banded chromosomes) described thus far for the vampires that provide synapomorphies for their relationship to the remainder of the phyllostomids.

We do not interpret the low level of support for deep branches in the total-evidence tree as robust evidence for monophyly of several higher-level taxa proposed by Wetterer et al. (2000; e.g., their subfamily Phyllostominae). Thus, in our view of their results, the majority of "incongruencies" between the molecular and total-evidence trees does not represent supported conflicts. For example, of the 18 nodes with bootstrap values ≥70%, 11 are present in the combined gene tree (nodes 11, 15, 21, 32, 39, 40, 48, 50, 51, 53, 55). Two others are not at conflict, but were not tested, due to differences in sampling (i.e., we did not analyze *Platalina* and *Phyllonycteris*). Only five clades represent supported conflicts between the combined gene tree and total-evidence tree: 1) the placement of *Lonchophylla, Lionycteris*, and *Platalina*

within the glossophagines; 2) the exclusion of *Erophylla*, *Phyllonycteris*, and *Brachyphylla* from the glossophagines; 3) a clade containing *Chiroderma, Vampyressa, Ectophylla*, and *Mesophylla*; 4) the sister-taxon relationship between *Centurio* and *Sphaeronycteris*; and 5) the sister-taxon relationship between *Lonchorhina* and *Macrophylum*.

Jones et al. (2002, pp. 240-241) state, "the phylogenetic signal in the Phyllostomidae supertree is strong and the topology is well resolved...The supertree supports the monophyly of 8 traditionally recognised subfamilies (Desmodontinae, Phyllostominae, Brachyphyllinae, Phyllonycterinae, Glossophaginae, Lonchophyllinae, Carolliinae, and Stenodermatinae)." However, such a conclusion is not verified by statistical (probablistic) support in their publication for any node or proposed taxon (Jones et al. 2002; see appendix 2 for decay values). It is important to understand the type of support that exists for the MRP tree. MRP trees (or "super"-trees) are not an analysis of primary data, but are a synthesis of the presence or absence of a clade in other studies (which may have been based on new primary data or a review of published data or both). Jones et al. (2002) did adjust their data set to help limit the redundancy of trees resulting from multiple publications of the same data set. However, the MRP method does not address a major concern of how much or how little support each clade had in the published trees. Few trees included in the MRP study were derived from explicit phylogenetic analysis and/or were accompanied by some measure of clade reliability (e.g., bootstrap or decay values). It is probable the MRP tree represents a synthesis of nodes presented in published dendrograms, of which many were without statistical support.

The above discussion brings into focus a critical feature of the data presented in this paper. First, the two gene trees, one from the mitochondrial genome and one from the nuclear genome, are strikingly similar in the deep branching patterns for this family of bats. Second, the two gene trees are strikingly different in deep branching patterns from the trees based primarily on anatomy, morphology, and chromosomes. There are three alternative hypotheses to explain these differences. Hypothesis one: the gene trees represent the most accurate phylogeny and the morphology trees are largely incorrect. Hypothesis two: the trees based on morphology represent the most accurate phylogeny and the gene trees are largely incorrect. Hypothesis three: neither the morphology nor the gene trees give an accurate representation of the phylogeny of this group of bats.

In light of the observation that one-third of all studies of bat systematics are on the phyllostomids (Jones et al. 2002), it might be expected that the phylogeny of the family would be well resolved, if the phylogeny of any bat family is well resolved. If hypothesis one proves to be most accurate, then why have the morphological studies been ineffective at resolving deep branching patterns in this family? Further, then are systematic inaccuracies in the phyllostomid tree based on morphology a unique problem to phyllostomid bats or is the phyllostomid data set a red flag warning of other inaccuracies for morphologically based studies of systematics? If hypothesis two proves to be most accurate, then our study will be a powerful setback for the hypothesis that congruent data from the mitochondrial or nuclear genomes (digenomic congruence) are among the most robust data available for systematic studies. If hypothesis three is most accurate, then the results of all previous studies of systematics are brought into question.

There are many incongruences among the digenomic tree (Fig. 5*a*), total-evidence tree (Fig. 1), and MRP tree (Fig. 2) that clearly merit further study. We do think, however, that the trees generated from the gene sequence data have a sufficiently high probability of reflecting the evolutionary relationships for this incredibly complex, morphological assemblage of bats, and that a classification based on these data is merited. The list of characters making these names available under Article 13 of the of the International Code of Zoological Nomenclature is the shared derived character states present in the mtDNA and *RAG2* DNA sequences as identified in a Bayesian analysis. As data analysis varies (choice of outgroups, model of evolution, taxon sampling, etc.) some details of the list of characters will change but the main body will remain. All sequences are available from GenBank.

It might seem that a classification would be simple to develop if the branching order of clades was as highly supported as is present in the molecular based trees. Nonetheless the assignment of taxonomic lev-

Table 2.—Classifications for the Phyllostomidae. * = Subgenus.

Miller 1907

Phyllostomidae
- Chilonycterinae (= Mormoopidae)
  - *Chilonycteris* (= *Pteronotus*, part)
  - *Mormoops*
  - *Pteronotus*
- Phyllostominae
  - *Micronycteris* (*megalotis*, *microtis*, *minuta*)
  - *Xenoctenes* (= *Micronycteris hirsuta*)
  - *Glyphonycteris*
  - *Otopterus* (= *Macrotus*)
  - *Lonchorhina*
  - *Dolichophyllum* (= *Macrophyllum*)
  - *Tonatia*
  - *Mimon* (*bennettii*)
  - *Anthorhina* (= *Mimon crenulatum*)
  - *Phyllostomus*
  - *Phylloderma*
  - *Trachops*
  - *Chrotopterus*
  - *Vampyrus* = *Vampyrum*
- Glossophaginae
  - *Glossophaga*
  - *Lonchophylla*
  - *Monophyllus*
  - *Anoura* (*geoffroyi*)
  - *Lonchoglossa* (= *Anoura caudifer*)
  - *Choeronycteris*
  - *Hylonycteris*
  - *Leptonycteris*
  - *Lichonycteris*
- Hemiderminae
  - *Hemiderma* (= *Carollia*)
  - *Rhinophylla*
- Sturnirinae
  - *Sturnira*
- Stenoderminae
  - *Brachyphylla*
  - *Uroderma*
  - *Vampyrops* (= *Platyrrhinus*)
  - *Vampyrodes*
  - *Vampyressa* (= *V. pusilla*)
  - *Vampyriscus* (= *V. bidens*)
  - *Chiroderma*
  - *Mesophylla*
  - *Ectophylla*
  - *Artibeus*
  - *Enchisthenes*
  - *Ardops*
  - *Phyllops*
  - *Ariteus*
  - *Stenoderma*
  - *Pygoderma*
  - *Centurio*
  - *Sphaeronycteris*
  - *Ametrida*
- Phyllonycterinae
  - *Phyllonycteris*
  - *Reithronycteris* (= *Phyllonycteris aphylla*)
  - *Erophylla*
- Desmodontidae
  - *Desmodus*
  - *Diaemus*
  - *Diphylla*

Baker et al. 1989

Phyllostomidae
- Desmodontinae
  - *Desmodus*
  - *Diaemus*
  - *Diphylla*
- *Macrotus* (*incertae sedis*)
- *Micronycteris* (*incertae sedis*)
- Vampyrinae
  - *Chrotopterus*
  - *Trachops*
  - *Vampyrum*
- Phyllostominae
  - Glossophagini
    - *Brachyphylla*
    - *Choeroniscus*
    - *Choeronycteris*
    - *Erophylla*
    - *Glossophaga*
    - *Hylonycteris*
    - *Leptonycteris*
    - *Lichonycteris*
    - *Lionycteris*
    - *Lonchophylla*
    - *Monophyllus*
    - *Musonycteris*
    - *Phyllonycteris*
    - *Platalina*
    - *Scleronycteris*
  - Phyllostomini
    - *Lonchorhina*
    - *Macrophyllum*
    - *Mimon*
    - *Phyllostomus* (includes *Phylloderma*)
    - *Tonatia*
  - Stenodermatini
    - *Ametrida*
    - *Ardops*
    - *Ariteus*
    - *Artibeus*
    - *Carollia*
    - *Centurio*
    - *Chiroderma*
    - *Dermanura* (includes *Enchisthenes*)
    - *Ectophylla*
    - *Pygoderma*
    - *Phyllops*
    - *Rhinophylla*
    - *Sphaeronycteris*
    - *Stenoderma*
    - *Sturnira*
    - *Uroderma*
    - *Vampyressa* (includes *Mesophylla*)
    - *Vampyrodes*
    - *Vampyrops* (= *Platyrrhinus*)

Koopman 1994

Phyllostomidae
- Phyllostominae
  - *Micronycteris*
    - **Micronycteris*
    - **Trinycteris*
    - **Neonycteris*
    - **Xenoctenes*
    - **Lampronycteris*
    - **Glyphonycteris*
    - **Barticonycteris*
  - *Macrotus*
  - *Lonchorhina*
  - *Macrophyllum*
  - *Tonatia*
  - *Mimon*
    - **Mimon*
    - **Anthorhina*
  - *Phyllostomus*
  - *Phylloderma*
  - *Trachops*
  - *Chrotopterus*
  - *Vampyrum*
- Lonchophyllinae
  - *Lionycteris*
  - *Lonchophylla*
  - *Platalina*
- Brachyphyllinae
  - *Brachyphylla*
- Phyllonycterinae
  - *Erophylla*
  - *Phyllonycteris*
    - **Phyllonycteris*
    - **Reithronycteris*
- Glossophaginae
  - *Glossophaga*
  - *Monophyllus*
  - *Lichonycteris*
  - *Leptonycteris*
  - *Anoura*
  - *Hylonycteris*
  - *Scleronycteris*
  - *Choeroniscus*
  - *Choeronycteris*
    - **Choeronycteris*
    - **Musonycteris*
- Carolliinae
  - *Carollia*
  - *Rhinophylla*
- Stenodermatinae
  - Sturnirini
    - *Sturnira*
      - **Sturnira*
      - **Corvira*
  - Sternodermatini
    - *Uroderma*
    - *Vampyrops* (= *Platyrrhinus*)
    - *Vampyrodes*
    - *Vampyressa*
      - **Vampyressa*
      - **Metavampyressa*
      - **Vampyriscus*
    - *Chiroderma*
    - *Mesophylla*
    - *Ectophylla*
    - *Artibeus*
      - **Artibeus*
      - **Enchisthenes*
      - **Dermanura*
    - *Ardops*
    - *Phyllops*
    - *Ariteus*
    - *Stenoderma*
    - *Pygoderma*
    - *Ametrida*
    - *Sphaeronycteris*
    - *Centurio*
- Desmodontinae
  - *Diphylla*
  - *Diaemus*
  - *Desmodus*

McKenna and Bell 1997

Phyllostomidae
- Phyllostominae
  - *Micronycteris*
  - *Macrotus*
  - *Lonchorhina*
  - *Macrophyllum*
  - *Tonatia*
  - *Mimon*
  - *Phyllostomus*
  - *Phylloderma*
  - *Trachops*
  - *Chrotopterus*
  - *Vampyrum*
- Glossophaginae
  - Brachyphyllini
    - *Brachyphylla*
  - Phylonycterini
    - *Erophylla*
    - *Phyllonycteris*
  - Glossophagini
    - *Glossophaga*
    - *Monophyllus*
    - *Lichonycteris*
    - *Leptonycteris*
    - *Anoura*
    - *Hylonycteris*
    - *Scleronycteris*
    - *Choeroniscus*
    - *Choeronycteris*
    - *Musonycteris*
  - Lonchophyllini
    - *Lionycteris*
    - *Lonchophylla*
    - *Platalina*
- Stenodermatinae
  - Carolliini
    - *Carollia*
    - *Rhinophylla*
  - Stenodermatini
    - Sturnirina
      - *Sturnira*
    - Stenodermatina
      - *Uroderma*
      - *Platyrrhinus*
      - *Vampyrodes*
      - *Vampyressa*
      - *Mesophylla*
      - *Ectophylla*
      - *Chiroderma*
      - *Artibeus*
      - *Ardops*
      - *Phyllops*
      - *Ariteus*
      - *Stenoderma*
      - *Pygoderma*
      - *Ametrida*
      - *Sphaeronycteris*
      - *Centurio*
- Desmodontinae
  - *Desmodus*
  - *Diaemus*
  - *Diphylla*

Table 2 (cont.)

Wetterer et al. (2000)

- Phyllostomidae
  - Desmodontinae
    - *Diphylla*
    - *Diaemus*
    - *Desmodus*
  - Brachyphyllinae (*incertae sedis*)
    - *Brachyphylla*
  - Hirsutaglossa (unranked taxon)
  - Glossophaginae
    - Glossophagini
      - *Anoura*
      - *Choeroniscus*
      - *Choeronycteris*
      - *Glossophaga*
      - *Hylonycteris*
      - *Leptonycteris*
      - *Lichonycteris*
      - *Monophyllus*
      - *Musonycteris*
      - *Scleronycteris*
    - Lonchophyllini
      - *Lionycteris*
      - *Lonchophylla*
      - *Platalina*
  - Phyllonycterinae
    - *Erophylla*
    - *Phyllonycteris*
  - Unnamed clade
  - Phyllostominae
    - Lonchorhinini
      - *Lonchorhina*
      - *Macrophyllum*
      - *Mimon*
    - Micronycterini
      - *Glyphonycteris*
      - *Lampronycteris*
      - *Macrotus*
      - *Micronycteris*
      - *Neonycteris*
      - *Trinycteris*
    - Phyllostomini
      - *Phylloderma*
      - *Phyllostomus*
    - Vampyrini
      - *Chrotopterus*
      - *Tonatia*
      - *Trachops*
      - *Vampyrum*
  - Nullicauda (unranked taxon)
  - Carolliinae
    - *Carollia*
    - *Rhinophylla*
  - Stenodermatinae
    - Stenodermatini
      - Ectophyllina
        - *Artibeus*
        - **Artibeus*
        - **Dermanura*
        - **Koopmania*
        - *Chiroderma*
        - *Ectophylla*
        - *Enchisthenes*
        - *Platyrrhinus*
        - *Uroderma*
        - *Vampyressa*
        - *Vampyrodes*
      - Stenodermatina
        - *Ametrida*
        - *Ardops*
        - *Ariteus*
        - *Centurio*
        - *Phyllops*
        - *Pygoderma*
        - *Sphaeronycteris*
        - *Stenoderma*
      - Sturnirini
        - *Sturnira*

Jones et al. (2000)

- Phyllostomidae
  - Desmodontinae
    - *Diphylla*
    - *Diaemus*
    - *Desmodus*
  - Phyllostominae
    - *Macrophyllum*
    - *Lonchorhina*
    - *Macrotus*
    - *Micronycteris*
    - *Trachops*
    - *Chrotopterus*
    - *Vampyrum*
    - *Tonatia*
    - *Mimon*
    - *Phylloderma*
    - *Phyllostomus*
  - Carolliinae
    - *Carollia*
    - *Rhinophylla*
  - Brachyphyllinae
    - *Brachyphylla*
  - Phylonycterinae
    - *Erophylla*
    - *Phyllonycteris*
  - Lonchophyllinae
    - *Platalina*
    - *Lionycteris*
    - *Lonchophylla*
  - Glossophaginae
    - *Leptonycteris*
    - *Monophyllus*
    - *Glossophaga*
    - *Anoura*
    - *Scleronycteris*
    - *Hylonycteris*
    - *Lichonycteris*
    - *Choeronycteris*
    - *Musonycteris*
    - *Choeroniscus*
  - Stenodermatinae
    - *Sturnira*
    - *Pygoderma*
    - *Centurio*
    - *Ametrida*
    - *Sphaeronycteris*
    - *Phyllops*
    - *Stenoderma*
    - *Ardops*
    - *Ariteus*
    - *Artibeus*
    - **Artibeus*
    - **Dermanura*
    - **Enchisthenes*
    - **Koopmania*
    - *Ectophylla*
    - *Chiroderma*
    - *Mesophylla*
    - *Vampyressa*
    - *Uroderma*
    - *Vampyrodes*
    - *Platyrrhinus*

Table 2 (cont.)

This Paper

Phyllostomidae
Macrotinae
Macrotus
Karyovarians (new, unranked taxon)
Micronycterinae
Micronycteris
Lampronycteris
Victivarians (new, unranked taxon)
Desmodontinae
Diphyllini
Diphylla
Desmodontini
Desmodus
Diaemus
Phyllovarians (new, unranked taxon)
Lonchorhininae
Lonchorhina
Unnamed, unranked taxon
Phyllostominae
Macrophyllini
Macrophyllum
Trachops
Phyllostomini
Lophostoma
Tonatia
Mimon
Phylloderma
Phyllostomus
Vampyrini
Chrotopterus
Vampyrum
Hirsutaglossa (unranked taxon)
Glossophaginae
Glossophagini
Monophyllus
Glossophaga
Leptonycteris
Brachyphyllini
Brachyphylla
Phyllonycterini
Erophylla
Phyllonycteris
Choeronycterini
Anourina
Anoura
Choeronycterina
Hylonycteris
Choeroniscus
Choeronycteris
Musonycteris
Lichonycteris
Scleronycteris
Dulcivarians (new, unranked taxon)
Lonchophyllinae
Lionycteris
Lonchophylla
Platalina
Nullicauda (unranked taxon)
Carolliinae
Carollia
Glyphonycterinae
Glyphonycteris
Trinycteris
Carpovarians (new, unranked taxon)
Rhinophyllinae
Rhinophylla
Stenodermatinae
Sturnirini
Sturnira
Stenodermatini
Vampyressina
Chiroderma
Vampyriscus
Uroderma
Vampyressa
Mesophylla
Vampyrodes
Platyrrhinus
Mesostenodermatini (new, unranked taxon)
Enchisthenina
Enchisthenes
Ectophyllina
Ectophylla
Artibeina
Artibeus
Dermanura
Stenodermatina
Ariteus
Ardops
Stenoderma
Centurio
Pygoderma
Sphaeronycteris
Ametrida
Phyllops

els to the gene trees was at times complicated and subjective. Our goal was to partition molecular and morphological data into taxa generally reflecting an equal level of evolutionary distance (Fig. 5*b*). In a previous classification, Baker et al. (1989) partitioned the variation into three subfamilies with one, the Phyllostominae, containing extensive diversity in morphological adaptations for feeding strategies. The feedback from mammalogists interested in the systematics of this family involved a consistent theme that the Baker et al. (1989) application of the subfamilial rank was not in agreement with its application among other mammalian families. Further feedback indicated that the magnitude of morphological variation within this family should be partitioned into a greater number of subfamilies. In the classification we propose here, we have attempted to reflect more closely the level of morphological variation associated with subfamilial rank in other mammalian families. Others who have proposed a classification for phyllostomid bats have also recognized more subfamilies than Baker et al. (1989): McKenna and Bell (1997) recognized four; Miller (1907), Koopman and Jones (1970), Corbet and Hill (1991), and Wetterer et al. (2000) recognized seven; and Griffiths (1982), Koopman (1993, 1994), and Jones et al. (2002) recognized eight. We recognize 11 subfamilies in order to partition the major morphological and genetic subdivisions into monophyletic groups.

CLASSIFICATION OF PHYLLOSTOMID BATS

Family: Phyllostomidae. This family is comprised of the same taxonomic assemblage as recognized by Forman et al. (1968), Baker et al. (1989), McKenna and Bell (1997), Koopman (1993, 1994), Wetterer et al. (2000), and Jones et al. (2002). All three gene trees, *RAG2* (Fig. 3), mtDNA (Fig. 4), and combined gene (Fig. 5), indicate monophyly of this previously recognized family. It might be tenable to argue that because this family contains more morphological and anatomical variation than any other family of mammals, as a means of standardizing such variation within the class Mammalia, this assemblage should be divided into two or more families. Doing so, however, would mask the significance of the evolutionary plasticity unique to this monophyletic group as well as the relative time frame of origin for this complex relative to other bat families. Within this family we recognize 11 subfamilies (Fig. 5*b*, Table 2).

Subfamily: Macrotinae. This subfamily is the basal clade of the Phyllostomidae and includes members of the genus *Macrotus*. Van Den Bussche (1992) was the first to classify *Macrotus* in its own separate subfamily. Baker et al. (1989) placed *Macrotus* as *incertae sedis* within the family, whereas Wetterer et al. (2000) placed it in the tribe Micronycterini. The statistical support for the exclusion of *Macrotus* from the remainder of the phyllostomids is the evidence for the monophyly of Karyovarians (node 2, Fig. 5*a*), which is present in the three molecular trees (Table 1).

Karyovarians: New, Unranked Taxon. We define this taxon as the clade (node 2, Fig. 5*a*) arising from the last common ancestor of *Micronycteris* (*sensu stricto*) and *Artibeus*. The taxon name is derived from the English *karyotype* and the Latin *varians*, meaning "diversifying." This taxon is named in recognition of the exceptional karyotypic variation present within its taxa. The one phyllostomid genus, *Macrotus*, not present in this taxon has a species, *M. waterhousii*, with a karyotype proposed as primitive for the family (Patton and Baker 1978; Baker 1979).

Subfamily: Micronycterinae. This subfamily is defined as the clade (node 52, Fig. 5*a*) arising from the last common ancestor of *Lampronycteris* and *Micronycteris* (*sensu* Wetterer et al. 2000). The subfamily Micronycterinae was first recognized by Van Den Bussche (1992); however, the composition of the subfamily was broader (included *Trinycteris* and *Glyphonycteris*) in his classification. The genus *Micronycteris* (*sensu* Koopman 1993) was placed as *incertae sedis* within the family by Baker et al. (1989).

Some comments on the generic status of *Micronycteris* are warranted. Sanborn (1949) recognized six subgenera (*Micronycteris, Lampronycteris, Xenoctenes Trinycteris, Glyphonycteris*, and *Neonycteris*) in the genus *Micronycteris*. With the addition of *Barticonycteris*, this subgeneric arrangement was followed by Koopman (1993, 1994). Wetterer et

al. (2000, p. 141) elevated five (*Micronycteris*, *Lampronycteris*, *Trinycteris*, *Glyphonycteris*, *Neonycteris*) of Sanborn's subgenera to generic status (See also Simmons and Voss 1998 and Simmons 1996). The Koopman (1993, 1994) composition of the genus was recreated from the MRP database of Jones et al. (2002; Fig. 2), and they placed all five subgenera into a single genus. The data from both the *RAG2* and mtDNA genes clearly indicate that the Sanborn (1949), Koopman (1993, 1994), and Jones et al. (2002) concept of *Micronycteris* is not monophyletic. Minimally, *Micronycteris* and *Glyphonycteris* must be recognized. We conclude that *Lampronycteris* is most appropriately recognized as a genus distinct from *Micronycteris* because of the arguments of Wetterer et al. (2000) and also because of the genetic distance (Fig. 5*b*) between them is typical of that distinguishing other closely related genera within the Phyllostomidae. We also follow Wetterer et al. (2000) in recognizing the genera *Glyphonycteris* and *Trinycteris* although the genetic distance separating them is slightly less than that separating *Lampronycteris* and *Micronycteris* (*sensu stricto*; Fig. 5*b*). No molecular data are available for *Neonycteris* and presently the generic status of this taxon must be viewed entirely on morphological variation.

Victivarians: New Unranked Taxon. This taxon is defined as the clade (node 3, Fig. 5*a*) arising from the last common ancestor of *Desmodus* and *Artibeus* (Fig. 5*a*, clade 2). The name of this taxon is derived from the Latin *victus* (meaning both "food" and "livelihood" or "lifestyle") and *varians* (meaning "diversifying"). This taxon is named in recognition of the diversity of feeding lifestyles, which is the greatest variation in feeding strategies present in any mammalian family.

Subfamily: Desmodontinae. This three-genus taxon (node 50, Fig. 5*a*) is defined as the clade arising from the last common ancestor of *Diphylla* and *Desmodus*. This taxon has been recognized in most (if not all) previous classifications either as a family (Miller 1907) or subfamily (Forman et al. 1968).

Tribe Diphyllini. As proposed, this tribe is monotypic. Although studies have recognized *Diphylla* as the basal branch in the vampires, the strongest support for separate taxonomic recognition is the molecular distance in the mtDNA, *RAG2*, and combined gene trees (Figs. 3-5). *Diphylla* has the greatest molecular distance for any genus or pair of genera in the combined gene tree (Fig. 5*a*), which we interpret as indicating an early divergence and substantial period of isolation for *Diphylla* relative to the other two genera of vampires (even if there is a faster rate of molecular evolution). The depth of the node uniting *Diphylla* to the *Desmodus*+*Diaemus* clade equals that of most nodes interpreted as justifying subfamilial status (Fig.5*b*).

Tribe: Desmodontini. This tribe is defined as the clade (node 51, Fig. 5*a*) arising from the last common ancestor of *Desmodus* and *Diaemus*. Most studies have found a sister relationship between *Desmodus* and *Diaemus* (see Jones et al. 2002).

Phyllovarians: New Unranked Taxon. This taxon is defined as the clade (node 4, Fig. 5*a*) arising from the last common ancestor of *Lonchorhina*, *Vampyrum,* and *Artibeus*. The name is derived from the Greek *phyllo* (meaning "leaf") and the Latin *varians* (meaning "diversifying"). This taxon is named in recognition of the extensive variation present in morphology of the nose-leaf. Whereas the deep branches of the phyllostomid tree always have been difficult to resolve (i.e., with concomitant statistical support), mitochondrial and nuclear data separately and combined support (posterior probability = 0.96 for all three datasets) the monophyly and an early divergence of Phyllovarians.

Subfamily: Lonchorhininae. This subfamily (Fig. 5*a*, the basal branch of clade 4), previously unrecognized, is defined as the clade arising from the last common ancestor of members of the genus *Lonchorhina*. The position of *Lonchorhina* within Phyllovarians differs, however, between our three trees. *Lonchorhina* is sister to *Lionycteris* and *Lonchophylla* in the *RAG2* tree, whereas *Lonchorhina* is positioned between the Glossophaginae and the common ancestor for the Carolliinae, Lonchophyllinae, Glyphonycterinae, Rhinophyllinae, and Stenodermatinae in the mtDNA tree. Both arrangements are not supported ($P<0.95$). The combined tree offers the greatest support (posterior probability of 0.96) for Lonchorhininae diverging from the remainder of the phyllostomids after divergence of the vampires but before the common ancestor of the re-

maining subfamilies (Phyllostominae, Glossophaginae, Lonchophyllinae, Carolliinae, Glyphonycterinae, Rhinophyllinae and Stenodermatinae; Fig. 5*a*). There is no obvious support for placing *Lonchorhina* with the remainder of the previously recognized Phyllostominae (*sensu* Wetterer et al. 2000; Koopman 1993, 1994; Jones et al. 2002). Placing *Lonchorhina* in another subfamily would require substantial rearrangements to produce a monophyletic group or, alternatively, would require a paraphyletic arrangement. The tribe Lonchorhinini was proposed by Wetterer et al. (2000), but included three genera; *Lonchorhina, Macrophyllum*, and *Mimon*. Our data do not support monophyly of Lonchorhinini (*sensu* Wetterer et al. 2000).

Unnamed: Unranked Taxon. This taxon is identified as the clade (node 5, Fig. 5*a*) arising from the last common ancestor for *Vampyrum* and *Artibeus*, and includes subfamily Phyllostominae and the six subfamilies within Hirsutaglossa (*sensu* this paper).

Subfamily: Phyllostominae. This subfamily is defined as the clade (node 42, Fig. 5*a*) arising from the last common ancestor for *Trachops*, *Vampyrum*, and *Phyllostomus*. It has been recognized in all previous classifications; however, herein the content is changed substantially and includes nine genera (*Chrotopterus, Lophostoma, Macrophyllum, Mimon, Phylloderma, Phyllostomus, Trachops, Tonatia*, and *Vampyrum*), the fewest number of genera proposed in any classification. Notably, the genera *Macrotus*, *Micronycteris*, *Lampronycteris*, *Lonchorhina*, *Trinycteris*, and *Glyphonycteris* are removed and classified into four other subfamilies.

Tribe: Phyllostomini. This tribe is defined as the clade (node 44, Fig. 5*a*) arising from the last common ancestor for *Tonatia* and *Phyllostomus* and contains five genera (*Mimon, Phylloderma, Phyllostomus, Lophostoma, Tonatia)*. Monophyly of Phyllostomini was supported in the combined and *RAG2* gene trees with a Bayesian probability of 1.00. The total-evidence tree of Wetterer et al. (2000) does not provide support for this tribe.

Tribe: Macrophyllini. This tribe is defined as the clade (node 49, Fig. 5*a*) arising from the last common ancestor for *Trachops* and *Macrophyllum* and contains only these two genera. Monophyly of Macrophyllini was supported with a probability of 1.00 in the combined and *RAG2* gene trees (Table 1). No association between *Macrophyllum* and *Trachops* to the exclusion of other genera in the Phyllostominae is present in the total-evidence tree of Wetterer et al. (2000) or has been previously proposed. Bats of these genera feed from the surface of pools of water, although by different means. *Trachops* feeds by catching frogs with their mouth, whereas *Macrophyllum* gaffes insects from the water surface with its feet (Gardner 1977b).

Tribe: Vampyrini. This tribe is defined as the clade (node 48, Fig. 5*a*) arising from the last common ancestor for *Chrotopterus* and *Vampyrum* and contains only these two genera. Monophyly of Vampyrini was supported in the combined and *RAG2* gene trees with a probability of 1.00. *Chrotopterus* and *Vampyrum* were recognized as sister taxa in the total-evidence tree of Wetterer et al. (2000).

Hirsutaglossa: Unranked Taxon. This taxon was defined (Wetterer et al. 2000) as the clade (node 6, Fig. 5*a*) arising from the last common ancestor of the Phyllonycterinae and the Glossophaginae (including *Lonchophylla*). Because Wetterer et al. (2000) included *Lonchophylla* in their definition of Glossophaginae, it places the definition of Hirsutaglossa to node 6 (Fig. 5*a*). This clade appears in the mtDNA and the combined gene trees. Within the Hirsutaglossa, we recognize six subfamilies.

Subfamily: Glossophaginae. We define the Glossophaginae as the clade (node 33, Fig. 5*a*) arising from the last common ancestor of *Choeronycteris*, *Brachyphylla*, and *Glossophaga*. This subfamily is composed of genera that, based on morphological divergence, were divided into three subfamilies (Brachyphyllinae, Glossophaginae, Phyllonycterinae) by Griffiths (1982) and Koopman (1993, 1994). The inclusion of *Brachyphylla, Erophylla* and *Phyllonycteris* was suggested by Baker and Bass (1979). Wetterer et al. (2000) divided these taxa into two subfamilies with *Brachyphylla* placed as *incertae sedis*. McKenna and Bell (1997) recognized these taxa as the tribes Brachyphillini, Glossophagini, and Phyllonycterini, which is similar to our arrangement except that these authors included 10 genera in the Glossophagini,

whereas we include three. McKenna and Bell (1997) also included the Lonchophyllini, which we recognize as a separate subfamily. In addition to these differences, the gene trees support the removal of *Lonchophylla* and *Lionycteris* from the Glossophaginae (as proposed by Griffiths 1982; but see Carstens et al. 2002 for an alternative tree).

Our mtDNA and *RAG2* trees support *Brachyphylla* and representatives of the Phyllonycterinae within Glossophaginae (*sensu* Griffiths 1982; Koopman 1993, 1994; Wetterer et al. 2000). Further, *Brachyphylla* and *Erophylla* are within a subclade (node 34, Fig. 5*a*) including *Glossophaga*, *Monophyllus*, and *Leptonycteris* to the exclusion of the remainder of the Glossophaginae (*sensu* this paper). This branching pattern was produced for these genera in Carstens et al. (2002; their Fig. 5*a*, p. 34) when these authors excluded characters associated with nectar feeding. G-band chromosomes also document that *Brachyphylla*, *Phyllonycteris*, *Erophylla*, *Glossophaga*, *Leptonycteris* and *Monophyllus* share a common ancestry (Baker and Bass 1979; Haiduk and Baker 1982), but the chromosomal data are inadequate to resolve whether the karyotype shared by these six genera is primitive for all glossophagines or if it represents a synapomorphy for only these six genera. The placement of the origin of this derived karyotype still remains unresolved.

Within the Glossophaginae, we recognize two major clades. One contains five genera without zygomatic arches and lower incisors (node 38; Fig. 5*a*; Carstens et al. 2002). The other (node 34, Fig. 5*a*) contains six genera, *Brachyphylla, Phyllonycteris, Erophylla, Glossophaga, Leptonycteris,* and *Monophyllus*, that often have been classified in three different subfamilies. As discussed below, one of these clades contains more morphological variation than is normally found in an internal clade in a mammalian subfamily, whereas the other clade contains substantially less morphological diversity. It is problematic to partition this variation into a Linnean classification. Below, we present our justification for our taxonomic placements.

Tribe: Glossophagini. This tribe is defined as the clade (node 35, Fig. 5*a*) arising from the last common ancestor for the genera *Glossophaga, Leptonycteris,* and *Monophyllus*, and contains only these three genera. The taxonomic content and context of this tribe has varied more than any other proposed tribe in the family. For example, Baker et al. (1989) recognized 15 genera within Glossophagini, which is equivalent to our subfamily Glossophaginae. Wetterer et al. (2000) recognized 10 genera in their Glossophagini. Based on the branching order in all three molecular trees, if we were to include additional genera within Glossophagini, we would be forced to include *Erophylla, Phyllonycteris*, and *Brachyphylla*. Herein lies one of the complications of developing this classification. As the result of extensive systematic study of classical morphological characteristics (Miller 1907; Griffiths 1982; Koopman 1993, 1994; Wetterer et al. 2000) *Brachyphylla* has been placed in the subfamily Brachyphyllinae and *Phyllonycteris* and *Erophylla* in the subfamily Phyllonycterinae. Our data support (posterior probability = 0.96) a shared common ancestry for *Brachyphylla, Phyllonycteris, Erophylla, Leptonycteris, Monophyllus*, and *Glossophaga* to the exclusion of all other phyllostomids (genetic data for *Phyllonycteris* are limited to the *RAG2* gene), and we recognize the morphological distinctiveness that was the basis for subfamilial recognition in previous classifications by according tribe status to the Glossophagini, Brachyphyllini, and Phyllonycterini. McKenna and Bell (1997) recognized these three tribes; however, the composition of the Glossophagini differed substantially.

Tribe: Brachyphyllini. This tribe contains a single genus with two species. As noted above, the tribe has been accorded subfamilial status in several other classifications (see Wetterer et al. 2000 for review). Morphologically, *Brachyphylla* has been associated with the Stenodermatinae (Dobson 1875; Miller 1907).

Tribe: Phyllonycterini. This tribe is defined as the clade arising from the last common ancestor for *Erophylla* and *Phyllonycteris*. See discussion under Glossophagini for justification.

Tribe: Choeronycterini. This tribe is defined as the clade (node 38, Fig. 5*a*) arising from the last common ancestor for *Anoura* and *Choeronycteris*. It includes *Anoura*, *Hylonycteris*, *Choeroniscus*, *Choeronycteris*, and *Musonycteris* (and probably

Lichonycteris and *Scleronycteris*). This clade was recognized by Carstens et al. (2002) in both of their summary trees (their Figs. 4 and 5). The branching order of the internal genera was identical to the order shown in our combined gene tree (Fig. 5). Based on genetic distances the rate of molecular evolution in Choeronycterini appears to be among the fastest within the family. This accelerated rate of molecular evolution is most apparent in the Choeronycterina as defined below. Morphologically, the Choeronycterini shares an absence of lower incisors and an incomplete zygomatic arch.

Subtribe: Anourina. This subtribe is defined as the last common ancestor shared by members of the genus *Anoura*. It includes a single genus and five species.

Subtribe: Choeronycterina. This subtribe comprises the clade (node 39, Fig. 5*a*) arising from the last common ancestor of *Hylonycteris* and *Choeronycteris*. It includes six genera and represents the ultimate modification in length of tongue and rostrum associated with nectar feeding within the Glossophaginae. No molecular data are available for the genera *Scleronycteris* and *Lichonycteris*, but on a morphological basis (Wetterer et al. 2000) they probably belong in this subtribe.

Dulcivarians: (New, Unranked Taxon). This taxon (node 7, Fig. 5*a*) is recognized as the last common ancestor of *Lonchophylla* and *Artibeus*. Support for this node is present in both the mtDNA and combined gene trees. The name is derived from the Latin *dulcis* (meaning "sweet") and *varians* (meaning "diversifying"). The name is given in recognition of the fact that the members of this taxon, which we divide into five subfamilies, feed predominantly on fruit and nectar.

Subfamily: Lonchophyllinae. This subfamily is defined as the clade (node 32, Fig. 5*a*) arising from the last common ancestor of *Lionycteris, Lonchophylla*, and *Platalina*. Considerable debate (Griffiths 1982, 1983; Haiduk and Baker 1982; Warner 1983; Smith and Hood 1984; Wetterer et al. 2000) has surrounded the correct taxonomic placement of these nectar-feeding bats. Bayesian analysis of the *RAG2* gene does not resolve the question of the monophyly of the Glossophaginae (*sensu* Miller 1907 and Wetterer et al. 2000). However, Bayesian analysis of the mtDNA data and the combined gene data both provide statistical support for the conclusion that *Lionycteris* and *Lonchophylla* did not share a common ancestry with the Glossophaginae (*sensu* this paper) to the exclusion of the remainder of the family. Therefore, we follow Griffiths (1982) in recognizing the Lonchophyllinae. Although no molecular data are available for *Platalina*, morphological similarities indicate that this is the proper clade in which this genus should be placed (Wetterer et al. 2000).

Nullicauda: (Unranked Taxon). This taxon was defined by Wetterer et al. (2000) as the clade arising from the last common ancestor of the Carolliinae and Stenodermatinae. We follow their definition in our classification; although in our phylogeny, this clade (node 8, Fig. 5*a*) includes taxa (*Trinycteris* and *Glyphonycteris*) not included in Nullicauda by Wetterer et al. (2000).

Subfamily: Carolliinae. This subfamily contains only the genus *Carollia* and is defined as the sister clade to node 30 (Fig. 5*a*) arising from the last common ancestor for members of the genus *Carollia*. There is support in the Bayesian trees from the *RAG2* and the combined gene data (Table 1) for the phylogenetic hypothesis that *Carollia, Glyphonycteris*, and *Trinycteris* shared a common ancestor after diverging from the remainder of the phyllostomid genera. Within the mtDNA tree, there is support for the hypothesis that *Carollia*, *Glyphonycteris*, and *Trinycteris* shared a common ancestry with *Rhinophylla* and the Stenodermatinae. However, unlike the *RAG2* data, the Lonchophyllinae is also present in this clade. There is no significant statistical support for the branching order present in the *RAG2* tree. We take a conservative approach and recognize the Carolliinae as a subfamily but not the clade giving rise to the *Carollia* + *Glyphonycteris* association.

Subfamily: Glyphonycterinae. This taxon is defined as the clade (node 30, Fig. 5*a*) arising from the last common ancestor of *Glyphonycteris* and *Trinycteris*, the only two genera recognized in this subfamily. *Barticonycteris* was recognized as congeneric with *Glyphonycteris* (Wetterer et al. 2000). The phylogenetic placement of these two taxa is perhaps the

greatest surprise of the molecular data. Species of both genera always have been placed in close association with those of *Micronycteris*, either within the same genus (Miller 1907; Sanborn 1949; Baker et al. 1989; Koopman 1993, 1994; McKenna and Bell 1997; Jones et al. 2002) or tribe (Micronycterini, Wetterer et al. 2000). If further study documents monophyly of Glyphonycterinae and Carolliinae to the exclusion of the remainder of the family, it may be appropriate to reduce these to a single subfamily. This, however, would be more consistent with the remainder of this classification if there were morphological synapomorphies defining their common ancestry.

Carpovarians (New, Unranked Taxon): This taxon is defined as the clade (node 9; Fig. 5*a*) arising from the last common ancestor of *Rhinophylla* and the Stenodermatinae. This name is derived from the Greek *karpos* (meaning "fruit") and the Latin *varians* (meaning "diversifying") in recognition of the diversity of fruit consumed by members of the clade. Carpovarians represents an enormously diverse group of bats, which we divide into two subfamilies.

Subfamily: Rhinophyllinae. This subfamily is defined as the last common ancestor shared by the species of the genus *Rhinophylla*. Previously, this genus has been associated with *Carollia* in the Carolliinae. The most favorable alternative to recognizing the Rhinophyllinae would be to place this genus in the Stenodermatinae at the tribe level.

Subfamily: Stenodermatinae. This subfamily is defined as the clade (node 10, Fig. 5*a*) arising from the last common ancestor of *Sturnira* and *Stenoderma*. The amount of biodiversity in number of species (62) and genera (20) is the greatest for any subfamily in our classification or those of Wetterer et al. (2000) or Jones et al. (2002). Based on branch lengths and their order in the gene trees, the Stenodermatinae is the most recently evolved of the subfamilies in this family. The monophyly of this subfamily as well as most internal clades are strongly supported (Fig. 5*a*). However, placing taxonomic names for the levels between the generic and tribe levels is difficult to standardize. We recognize two tribes within this subfamily.

Tribe: Sturnirini. This tribe contains the genus *Sturnira* and is defined as the clade arising from the last common ancestor of the genus (the basal divergence from clade 10; Fig. 5*a*). This tribe was recognized by Koopman (1994) and Wetterer et al. (2000) and was accorded subfamilial rank by Miller (1907) but was placed within the Stenodermatinae by Baker (1967) based on chromosomal data.

Tribe: Stenodermatini. This tribe is defined as the clade (node 11, Fig. 5*a*) arising from the last common ancestor of *Vampyressa* and *Ametrida*. It comprises 19 genera and at least 50 species. Within this tribe, there are two major clades supported in the *RAG2*, mtDNA, and combined gene trees.

Subtribe: Vampyressina. This taxon is defined as the clade (node 22, Fig. 5*a*) arising from the last common ancestor of *Chiroderma, Platyrrhinus, Vampyrodes, Uroderma, Mesophylla, Vampyressa*, and *Vampyriscus*. We recognize *Vampyriscus* as a distinct genus from *Vampyressa* because of the placement of *Vampyriscus brocki* and *Vampyriscus bidens* in the three gene trees. The type species for *Vampyressa* is *V. pusilla*, and the generic name *Vampyriscus* was proposed for *Vampyressa bidens* (Thomas 1900). In both gene trees, *V. brocki* and *V. bidens* are sister, and the conservative approach would be to place both species in the same genus. The systematic placement of *V. nymphaea* is not resolved by our data. A close relationship between *Vampyressa nymphaea* and *Mesophylla* was proposed by Owen (1987). In the gene trees, *Mesophylla macconnelli* is sister to *Vampyressa thyone* (not *Ectophylla alba)*. Chromosomal data also are explained most-parsimoniously by a relationship between *Vampyressa thyone* and *M. macconnelli* relative to the other Vampyressina genera. In light of these data, we recognize the genus *Mesophylla (*including only *M. macconnelli)*, place it in the subtribe Vampyressina, and consider it to be sister to *Vampyressa thyone* or possibly to a clade comprised of *V. thyone, V. pusilla*, and *V. melissa* (for which no molecular data are available). Lim et al. (2003) arranged *Ectophylla* and *Mesophylla* as sister and explained the chromosomal similarities (Baker et al. 1973, Greenbaum et al. 1975) as convergent evolution following Gardner (1977a). The branching pattern in figure 5 is not parsimoniously compatible with Gardner's hypothesis concerning the primitive karyotype for the family. With *Mesophylla* and *Vampyressa thyone* being arranged as in figure 5, there is no need to invoke convergent chromosomal evolution as an explanation.

Mesostenodermatini: (New, Unranked Taxon.) This taxon is described as the clade (node 12, Fig. 5*a*) arising from the last common ancestor for *Ectophylla, Enchisthenes,* and *Ametrida*. This name is derived from the Greek *meso* (meaning "middle") and the tribe name, Stenodermantini, because this taxon forms a middle clade within the Stenodermatini. Within this taxon, we recognize four subtribes: the Stenodermatina, Enchisthenina, Ectophyllina, and Artibeina.

Subtribe: Enchisthenina. This subtribe is comprised of the monotypic genus *Enchisthenes* and is defined as the last common ancestor for members of *Enchisthenes hartii* as currently defined. Jones et al. (2002) placed *E. hartii* as a congener of *Artibeus*. Our data from both the nuclear and the mitochondrial genomes indicate that *Enchisthenes* is not a member of the genus *Artibeus*. This conclusion was also drawn by Van Den Bussche et al. (1998) and Wetterer et al. (2000).

Subtribe: Ectophyllina. This subtribe is comprised of the monotypic genus *Ectophylla* and is defined as the last common ancestor for individuals of *Ectophylla*. In some other classifications (reviewed in Wetterer et al. 2000), *Ectophylla* is thought to contain two species: *E. alba* and *E. (Mesophylla) macconnelli*. However, as defended below *Mesophylla* appears to be sister to *Vampyressa thyone* and is not included in this subtribe.

Subtribe: Artibeina. This subtribe is defined as the clade (node 21, Fig. 5*a*) arising from the last common ancestor of *Artibeus* and *Dermanura*. Van Den Bussche et al. (1998) and Wetterer et al. (2000) regard *Koopmania* as a junior synonym of *Artibeus*.

Subtribe: Stenodermatina. This taxon is defined as the clade (node 15, Fig. 5*a*) arising from the last common ancestor of *Ariteus*, *Stenoderma,* and *Ametrida*. This group of bats has been identified morphologically as the short-faced bats, and the monophyly of this group has been proposed in nearly all classifications. Unlike previous studies, *Enchisthenes, Ectophylla, Dermanura*, and *Artibeus* are allied with the Stenodermatina as basal divergences. The alternatives are to expand the Stenodermatina to include these other four genera or to erect subtribes for them. The branching pattern for the clades at the base of the Stenodermatina requires the recognition of three subtribes if *Enchisthenes, Ectophylla, Dermanura*, and *Artibeus* are not placed in the subtribe Stenodermatina.

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*Appendix 1.—List of specimens examined. Specimens were collected from natural populations and voucher specimens are housed at the American Museum of Natural History (AMNH), Carnegie Museum of Natural History (CM), Louisiana Museum of Natural History (LSU), Museo de Historia Natural, Universidad Nacional Mayor de San Marcos, Lima (MUSM), Muséum National d'Histoire Naturalle, Paris (MNHN), Museum of Southwestern Biology at the University of New Mexico (MSB), Museum of Texas Tech University (TTU), United States National Museum of Natural History (USNM), Royal Ontario Museum, Toronto (ROM), Texas Cooperative Wildlife Collection at Texas A&M University (TCWC), Universidad Autónoma Metropolitana-Iztapalapa, Mexico City (UAM-I), or University of Wisconsin Zoological Museum (UWZM). ***Location of voucher specimen undetermined.*

Taxon	Tissue No.	Locality	Museum Voucher No.	GenBank Acc. No.
Ametrida centurio	TK 17741	Suriname: Saramacca: Geyskes Cr., Tafelberg	AMNH 267279	AY395802
Anoura caudifer	TK 55308	Peru: Cusco: La Convencion; Camisea, Pagoreni	USNM 582796	AY395835
Ardops nichollsi	TK 15602	Dominica: St. Joseph, Clarke Hall	TTU 31357	AY395803
Ariteus flavescens	TK 27696	Jamaica: St. Anne's Parish, Circle B Plantation, 2 km SW Priory	TTU 45291	AY395804
Artibeus obscurus	TK 17080	Suriname: Nickerie, Kayserberg Airstrip	CM 68951	AY395805
Artibeus jamaicensis	AMNH 267998		AMNH 267998	AF263225
Artibeus jamaicensis	AMNH 267999		AMNH 267999	AF263226
Brachyphylla cavernarum	TK 21807	Puerto Rico: Naguabo: Caribbean National Forest	TTU 46380	AY395806
Carollia perspicillata	TK 19368	Venezuela: Merida: Merida	CM 78421	AY395836
Centurio senex	TK 13537	Mexico: Yucatan	***	AF263227
Chiroderma salvini	TK 70524	Peru: Cusco: La Convencion; Camisea, Pagoreni	MUSM 13611	AY395837
Chiroderma trinitatum	TK 55323	Peru: Cusco: La Convencion; Camisea, Pagoreni	USNM 577863	AY395807
Choeronycteris mexicana	TK 20501	Mexico: San Luis Potosi: 15 mi. S, 1 mi. E Huizache	TTU 36118	AY395808
Choeroniscus minor	TK 70471	Peru: Cusco: La Convencion; Armihuari	USNM 577764	AY395809
Chrotopterus auritus	TK 70457	Peru: Cusco: La Convencion; Armihuari	MUSM 13653	AF411538
Dermanura cinerea	TK 18790	French Guiana: Paracou; near Sinnamary	AMNH 267197 MNHN 1995.1110	AY395810
Desmodus rotundus	TK 4764	Mexico: Guerrero: 24.1 mi. N Rio Union	TTU 35582	AF263228
Diaemus youngi	TK 34625	El Salvador: La Paz: 1 mi. N La Herradura	TTU 62792	AF411534
Diphylla ecaudata	TK 13514	Mexico: Yucatan: 1 km N. Merida	***	AF411533
Ectophylla alba	TK 16395	Costa Rica: Cano Palma Biological Station, 7km NNW Tortuguerro	ROM 108296	AY395811
Enchisthenes hartii	TK 55331	Peru: Cusco: La Convencion; Camisea, Armihuari	USNM 582822	AY395838
Erophylla sezekorni	TK 9416	Jamaica: Hanover Parrish, Flint River, 1.5 mi. E Sandy Bay	CM 44113	AY395839
Furipterus horrens	AMNH 272837	French Guiana: Paracou	AMNH 272837	AF345921

Appendix 1 (cont.)

Taxon	Tissue No.	Locality	Museum Voucher No.	GenBank Acc. No.
Glossophaga soricina	TK 70461	Peru: Cusco: La Convencion; Camisea, Armihuari	MUSM 13718	AY395840
Glyphonycteris daviesi	TK 16370	Ecuador: Napo: 42 km S, 1 km E Pompeya Sur (Parque Nacional Yasuni)	ROM 104042	AY395812
Glyphonycteris sylvestris	TK 10461	Suriname: Brokopondo: Brownsberg Nature Park, 8 km S, 2 km W Brownsberg	CM 63598	AY395841
Hylonycteris underwoodi	TK 20540	Mexico: Tabasco: 3 km E Talpa	TTU 36152	AY395813
Lampronycteris brachyotis	TK 25238	Trinidad: Mayaro: Guayaguayare	TCWC	AF411536
Leptonycteris curasoae	TK 45108	Mexico: D.F.: 34 km S Cd. de México, La Cima	UAM-I	AY395814
Lionycteris spurrelli	TK 22541	Panama: Darien: Cana	LSU	AY395815
Lonchophylla handleyi	TK 55312	Peru: Cusco: La Convencion; Camisea, Pagoreni	MUSM 13728	AY395816
Lonchophylla thomasi	TK 55321	Peru: Cusco: La Convencion; Camisea, Pagoreni	USNM 577763	AY395842
Lonchorhina aurita	TK 20560	Mexico: Chiapas, 2.5 mi SE, 2.5 E El Manteco	TTU 36531	AY395843
Lonchorhina orinocensis	TK 16394	Venezuela: Amazonas: Pozon; 50km NE Puerto Ayachucho	ROM 43000	AY395817
Lophostoma brasiliense	TK 18834	French Guyana: Paracou	AMNH 267103	AF411544
Macrophyllum macrophyllum	TK 19119	Venezuela: Bolivar: 8 km S, 5 km E El Manteco	CM 78289	AF411540
Macrotus waterhousii	TK 32021	Cuba: Guantanamo Prov.; Guantanamo Bay Naval Station	TTU 52478	AF263229
Mesophylla macconnelli	TK 70491	Peru: Cusco: La Convencion; Armihuari	USNM 577949	AY395818
Micronycteris hirsuta	TK 25041	Trinidad: St. George, Simla Research Center, 4 mi N Arima	CM 97177	AY395819
Micronycteris homezi	TK 86643	Guyana: Berbice Dist.: Dubulay Ranch; 5° 40' 91" N; 57° 51' 52" W	***	AY395820
Micronycteris megalotis	TK 17071	Suriname: Nickerie, Kayserberg Airstrip	CM 68390	AY395821
Micronycteris microtis	TK 18782	French Guiana: Paracou; near Sinnamary	AMNH 267097	AY395822
Micronycteris minuta	TK 18781	French Guiana: Paracou; near Sinnamary	AMNH 267098	AY395823
Micronycteris c.f. schmidtorum	TK 70447	Peru: Cusco: La Convencion; Armihuari	MUSM 13737	AF411535
Mimon crenulatum	TK 25230	Trinidad and Tobago: Trinidad: Mayaro	CM 97186	AF411543
Monophyllus redmani	TK 27708	Jamaica: St. Ann's Parish, 2 km SW Priory	TTU 45277	AY395824
Mormoops megalophylla	TK 78661	USA: Texas: Brewster Co.; Black Gap Wildlife Management Area	TTU 79275	AF263220
Musonycteris harrisoni	TK 19556	Mexico: Jalisco: 2 mi. W Tomatlan	TTU 36433	AY395844

Appendix 1 (cont.)

Taxon	Tissue No.	Locality	Museum Voucher No.	GenBank Acc. No.
Mystacina tuberculata	UWZM-M 27027	New Zealand: North Island	UWZM-M 27027	AF263222
Noctilio albiventris	TK 86633	Guyana: Berbice District	***	AF263223
Noctilio leporinus	TK 10224	Suriname: Saramacca	CM 63552	AF263224
Phylloderma stenops	TK 10201	Suriname: Saramacca: Raleigh Falls	CM 63614	AF411542
Phyllostomus elongatus	TK 19289	Venezuela: Bolivar: 28 km E El Palmar	CM 78327	AF411541
Platyrrhinus brachycephalus	TK 55320	Peru: Cusco: La Convencion; Camisea, Pagoreni	MUSM 13791	AY395825
Pteronotus parnellii	AMNH 269115		AMNH 269115	AF263221
Pygoderma bilabiatum	TK 12682	Bolivia: Santa Cruz: San Rafael de Amboro; 17° 36' S; 63° 36' W	MSB 55894	AY395826
Rhinophylla pumilio	TK 17550	Suriname: Marowijne: 3 km SW Albina	CM 77388	AY395827
Saccopteryx bilineata	AMNH 267842	French Guiana: Paracou	AMNH 267842	AF263213
Sphaeronycteris toxophyllum	TK 55326	Peru: Cusco: La Convencion; Camisea, Pagoreni	USNM 577905	AY395828
Stenoderma rufum	TK 21786	Puerto Rico: Rio Grande: Caribbean National Forest	TTU 46373	AY395829
Sturnira magna	TK 70473	Peru: Cusco: La Convencion, Armihuari	USNM 577905	AY395845
Tonatia saurophila	ROM 103401		ROM 103401	AF 411530
Trachops cirrhosus	TK 18829	French Guyana: Paracou	AMNH 267129	AF411539
Trinycteris nicefori	TK 15189	Venezuela: Guarico: 45 km S Calobezo	***	AY395830
Uroderma bilobatum	TK 46006	Peru: Loreto: Quebrada Aguas Negras, Cocha Zoraida	***	AY395831
Vampyressa thyone	TK 70454	Peru: Cusco: La Convencion; Armihuari	MUSM 14059	AY395832
Vampyriscus bidens	TK 70451	Peru: Cusco: La Convencion; Armihuari	MUSM 14038	AY395833
Vampyriscus brocki	TK 10316	Suriname: Nickerie; 24 km S, 60 km E, Apoera (4°,41'N, 56°, 7'W)	CM 66871	AY395834
Vampyrodes caraccioli	TK 70540	Peru: Cusco: La Convencion; Camisea, Pagoreni	USNM 582872	AY395846
Vampyrum spectrum	TK 40370	Honduras: Atlantida	TTU 61071	AF411537

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By: Robert J. Baker, Steven R. Hoofer, Calvin A. Porter, and Ronald A. Van Den Bussche

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